Universidad Autónoma de Querétaro

Facultad de Ciencias Naturales.

Doctorado en Ciencias Biológicas.

Identificación individual de *Eira barbara* y patrones de actividad en poblaciones de vida libre a lo largo de su distribución.

Tesis

Que como parte de los requisitos para obtener el grado de
Doctor en Ciencias Biológicas

Presenta:
Álvaro José Villafañe Trujillo

Dirigido por:
Dr. Carlos Alberto López González

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RESUMEN

La relevancia de identificar individualmente a los miembros de una población ha sido documentada ampliamente en estudios de ecología y comportamiento de diferentes especies de mamíferos. Las cámaras trampa son una de las herramientas más útiles y versátiles en estudios de investigación biológica con fines de conservación. Las fotografías son utilizadas para identificar el uso del hábitat, describir el comportamiento, analizar patrones de actividad y generar descripciones poblacionales. En el primer estudio se planteó la interrogante respecto a la identificación individual de *Eira barbara* mediante el parche de color que presenta en la garganta. Se revisaron 275 ejemplares de colecciones zoológicas para analizar la variación morfológica de la mancha gular de organismos colectados en casi toda la distribución de la especie. Se encontraron diferencias en la forma y tamaño de los parches gulares, todos los ejemplares con este carácter pueden ser identificados individualmente. El criterio de identificación se aplicó a registros fotográficos de una población de vida libre del Amazonas Peruano. Se identificaron nueve organismos diferentes, con dos ejemplares recapturados, lo cual demuestra la utilidad del criterio de identificación propuesto. En el segundo estudio la interrogante consistió en identificar si existen variaciones en los patrones de actividad de *Eira barbara* a través de su distribución geográfica. Se analizaron 957 registros de cámaras trampas correspondientes a 10 poblaciones ubicadas desde el sur de México hasta el norte de Argentina. Se utilizó el estimador de densidad de Kernel para generar los patrones de actividad, se calculó el coeficiente de sobreposición (Δ) para estimar la proporción de sobreposición de actividad entre poblaciones. *Eira barbara* tiene hábitos principalmente diurnos en toda su distribución, se identificaron variaciones latitudinales en su actividad. En poblaciones del hemisferio norte el mayor pico de actividad ocurre en las primeras horas posteriores al amanecer, en poblaciones cercanas al Ecuador geográfico el único pico de actividad ocurre alrededor del mediodía, en poblaciones del hemisferio sur el pico de actividad ocurre en distintas horas diurnas. Los valores de sobreposición oscilaron entre $\Delta 4 = 0.64$ y $\Delta 1=0.95$, los cuales reflejan la variación en las horas de actividad de la especie en un gradiente latitudinal.

Palabras clave: Cámaras trampa, Carnívoro, Diurno, Mamífero escansorial, Monitoreo no invasivo, Mustelidae, Neotropical.

SUMMARY

The relevance of identifying individually the members of a population has been extensively documented in studies of ecology and behavior of different mammalian species. The camera traps are one of the tools most useful and versatile in biological research for the purpose of conservation. The photographs are used to identify the habitat use, describe the behavior, analyze the activity patterns and generate population descriptions. The objective of the first study, the question was raised regarding the individual identification of *Eira barbara* through the throat patch characteristics. We reviewed 275 specimens of zoological collections to analyze the morphological variations of the throat patch in specimens collected throughtout the species range. Differences were found in the shape and size of the throat patches, therefore all specimens with this character can be individually identified. The proposed identification criterion was applied to photographic records obtained from a free-living population of the Peruvian Amazon. Nine different individuals were identified, with two recaptured specimens, which demonstrate the usefulness of the proposed identification criterion. In the second study, the question was to identify the variations in the activity patterns of *Eira barbara* throughout their range. Were analyzed 957 camera records corresponding to 10 populations located from southern Mexico to northern Argentina. Kernel density activity estimator was used to generate the species activity patterns and estimates, the overlap coefficient (Δ) corresponding to the activity overlap between populations. *Eira barbara* was mainly diurnal behavior throughout its distribution while, latitudinal variations were identified. In the populations of the northern hemisphere the highest peak of activity occurs in the first hours after sunrise, in populations close to the geographical equator the peak of activity occurs around noon and, in the populations of the southern hemisphere the peak of activity occurred in different hours of the daylight phase. The overlap values ranged between $\Delta_4 = 0.64$ and $\Delta_1 = 0.95$, which indicates the variations of the species activity patterns in a latitudinal gradient.

Key Words: Camera-tramp, Carnivore, Diurnal, Mustelidae Neotropical, Non-Invasive survey, Scansorial mammal.

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PRÓLOGO

La presente tesis se encuentra dividida en dos capítulos, el primero: Throat Patch Variation in Tayra (*Eira barbara*) and The Potential for Individual Identification in the Field, fue enviado a la revista "Diversity" (EISSN 1424-2818), donde fue publicado el 24 de enero de 2018. El segundo capítulo: Activity patterns of tayra (*Eira barbara*) across their distribution, tiene el formato de la revista "Journal of Zoology".

Los dos capítulos mantienen la mayoría de normas editoriales acorde a la revista a la que fueron redactados, por lo que el formato es diferente respecto al tipo de fuente, interlineado y estilo de citación.

INTRODUCCIÓN GENERAL

El estudio de las poblaciones de mamíferos (mediante abundancia relativa y patrones de actividad) pueden ayudar a comprender la estructura de un ecosistema (Lira-Torres & Briones-Salas, 2012). En México las investigaciones acerca de las siete especies de mustélidos registrados (*Enhydra lutris*, *Lontra longicaudis*, *Galictis vittata*, *Eira barbara*, *Mustela frenata*, *Mustela nigripes* y *Taxidea taxus*) están enfocadas a múltiples cuestiones ecológicas tanto en poblaciones de vida libre como en poblaciones de cautiverio (Eldridge & Whitford, 2009; Garcia-Alaniz, Naranjo, & Mallory, 2010; Murillo, Aguilar, Naranjo, & Vazquez, 2011; Arellano Nicolás, Sánchez Núñez, & Mosqueda Cabrera, 2012; Garwood *et al.* 2013; Schramm *et al.* 2014).

Eira barbara es un mustélido neotropical distribuido desde el centro de México hasta el norte de Argentina (Hunter, 2011), es una especie poco estudiada, y se desconocen aspectos básicos de su ecología. A pesar de ser una especie amenazada (catalogada como especie de preocupación menor por la Unión Internacional para la Conservación de la Naturaleza y como especie en riesgo de extinción en México, NOM-059) las investigaciones con utilidad para la conservación de la especie son escasas. Los registros de *Eira barbara* disponibles en la literatura en su mayoría son resultados colaterales de investigaciones enfocadas a otras especies (Camargo & Ferrari, 2005; López-González & Aceves-Lara, 2007; Ramírez-Bravo, 2011; Pérez-Irineo & Santos-Moreno, 2012), los cuales se limitan a mencionar su presencia en la región.

Desde el 2014 hasta el 2018 se desarrollaron diferentes investigaciones (se revisaron especímenes de colecciones zoológicas, se realizaron monitoreos no invasivos a ejemplares en cautiverio y a poblaciones de vida libre y se revisaron bases de datos de monitoreos no invasivos) con el objetivo de producir información ecológica básica sobre la especie. Se generó un criterio de identificación individual para *Eira barbara*, el cual se aplicó en poblaciones de vida libre de México y Perú, se identificaron los patrones de actividad de la especie en 10 poblaciones de vida libre distribuidas a lo largo del continente americano (México, Belice, Costa Rica, Perú, Ecuador, Brasil y Argentina).

Eira barbara: descripción y distribución de la especie.

Eira barbara (también conocido en Norteamérica como viejo de monte, cabeza de viejo o tayra) es un mustélido escansorial (de hábitos terrestres y arborícolas) de tamaño mediano, su cuerpo es de forma alargada y delgada, aunque fuerte y ágil (Aranda, 2012). Tiene la espalda encorvada, extremidades anteriores y posteriores cortas, provistas de cinco garras no retráctiles, adaptadas para trepar árboles y correr, pero no para excavar ni nadar (Pocock, 1921). Un organismo adulto tiene una longitud total de entre 105 y 116 cm, de los cuales entre 36 y 42 cm corresponden a la cola (Aljure *et al.* 2006). Los machos adultos son 30% más grandes que las hembras (Kaufmann & Kaufmann, 1965; Poglayen-Neuwall, 1975).

Históricamente *Eira barbara* se encuentra distribuida desde las costas del centro de México hasta el norte de Argentina (Figura I-2; Hunter, 2011). Se considera que habita en selva alta, selva baja, bosques tropicales y subtropicales, así como bosques lluviosos (Jiménez *et al*. 2010), bosques de galería, bosques nublados, matorrales secos y sabanas. Altitudinalmente está distribuida desde cero hasta 2400 metros sobre el nivel del mar (Emmons & Freer, 1990), teóricamente es poco común a partir de los 1200 msnm (Eisenberg, 1989), en Ecuador existen registros de la especie entre los 2708 y los 3100 metros sobre el nivel del mar (Reyes-Puig *et al*. 2015).

A través de su distribución geográfica existen siete subespecies de *Eira barbara* las cuales difieren en tamaño y en el color del pelaje (Presley, 2000, Figura I-1):

- ✓ *E. b. barbara* (Linnaeus, 1758), el pelaje del cuerpo es color café opaco, la cabeza tiene un color entre grisácea y café, mancha gular (amarillenta) presente (Figura I-1-1), está distribuida aproximadamente en: Paraguay, parte de Brasil, Perú, Bolivia y Argentina.
- ✓ *E. b. sinuensis* (Humboldt, 1812), el pelaje del cuerpo es color negro, nuca color café, más oscura que la cabeza, la mancha gular puede o no estar presente (Figura I-1-2), está distribuida aproximadamente en: Panamá, parte de Costa Roca, Venezuela, Colombia y Ecuador.
- ✓ *E. b. poliocephala* (Traill, 1812), cuerpo color café opaco con partes grisáceas, cabeza color café. Parche gular presente, el cual puede extenderse por hombros y/o espalda (Figura I-1-3), está distribuida aproximadamente en: Guyana, Guyana Francesa, Surinam, parte de Brasil y Venezuela.
- ✓ *E. b. peruana* (Nehring, 1886), cuerpo color café oscuro, patas más oscuras que el cuerpo, presencia del parche gular no especificado (Figura I-1-4), está distribuida aproximadamente en: parte de Perú y Bolivia.
- ✓ *E. b. senex* (Thomas, 1900), cuerpo color negro o café oscuro, nuca color blanco grisáceo, mancha gular (amarillenta) presente (Figura I-1-5), está distribuida aproximadamente en: Belice, parte de México, Guatemala y Honduras.
- ✓ *E. b. inserta* (Allen, 1908), cuerpo negro, cabeza color café oscuro, no tiene mancha gular (Figura I-1-6), está distribuida aproximadamente en: El Salvador, Nicaragua, parte de Guatemala, Honduras y Costa Rica.

✓ *E. b. madeirensis* (Lunnberg, 1913), cuerpo color café oscuro, nuca ligeramente más clara que el resto del cuerpo, la mancha gular puede o no estar presente (Figura I-1-7), está distribuida aproximadamente en: arte de Brasil, Venezuela, Colombia, Perú y Ecuador.

Figura I-1. Fenotipos de las siete subespecies de *Eira barbara* reconocidas por Cabrera (1958), y Hall (1981); recopiladas por Presley (2000). Créditos fotografías: 1= Zoológico de Praga ©, 2= Nick Hawkins ©, 3 = Villafañe-Trujillo ©, 4= Joseph Kolowski ©, 5= Villafañe-Trujillo ©, 6= David Cook © y 7= Joel Sartore ©.

Figura I-2. Distribución geográfica de *Eira barbara* y sus subespecies según una modificación de los datos propuestos por Cabrera (1958), Hall (1981) y la Unión Internacional para la Conservación de la Naturaleza (IUCN, 2008).

En México el pelaje *de Eira barbara* es disruptivo (presenta colores contrastantes o marcas irregulares que rompen el contorno del cuerpo; Merilaita, 1998). El pelaje del dorso, vientre, extremidades y cola es de color café oscuro brilloso o negro, a excepción de cabeza y nuca que tienen un color grisáceo, marrón amarillento o café claro; las orejas son pequeñas y redondas (Emmons & Feer, 1999; Aquino *et al.* 2001).

Subespecies

La categoría taxonómica subespecie históricamente ha sido polémica y malentendida, el principal argumento en contra es que la designación de subespecie es arbitraria (Patten, 2015). El concepto de subespecie ha sido definido como: el conjunto de poblaciones que ocupan un rango distintivo de reproducción y que se distingue claramente de otras poblaciones similares (estas poblaciones contienen individuos totalmente fértiles, las poblaciones no están reproductivamente aisladas; Mayr, 1942).

En algunos casos (anteriores al siglo XXI) la clasificación de un organismo como una subespecie está basada en diferencias morfológicas y craneométricas (Ruiz-García & Pinedo-Castro, 2013). De acuerdo con Avise y Ball (1990), la designación de subespecies debe hacerse con base en distribuciones concordantes de múltiples rasgos independientes (genéticos).

En el caso de *Eira barbara* la designación de diferentes subespecies ocurrió desde mediados del siglo XVIII hasta inicios del siglo XX, las cuales estuvieron basadas principalmente en diferencias anatómicas, de distribución geográfica y por el color del pelaje. Autores posteriores siguieron empleando estas clasificaciones a pesar de no estar basadas en análisis genéticos que los respaldaran.

Actualmente la única reconstrucción filogenética de *Eira barbara* es la reportada por Ruiz-García *et al*., (2013), cuyos resultados moleculares sugieren que en Sudamérica existen dos subespecies de *Eira barbara*: *barbara* (formada por los grupos reconocidos como: *barbara*, *peruana*, *sinuensis* y *madeirensis*) y *poliocephala*. Hasta el momento distintos autores han documentado la existencia de cinco variaciones fenotípicas de la especie (sin contar al fenotipo de pelaje blanco-amarillento presente en Guyana y Brasil) distribuidos desde Panamá hasta Argentina, estas variaciones en el color del pelaje son reconocidas genéticamente como dos subespecies de *Eira barbara*. Se desconoce si las poblaciones distribuidas desde México hasta Panamá corresponden a alguna de las subespecies reportadas para Sudamérica o si son diferentes a las propuestas por Ruiz-García *et al*., (2013).

Los métodos filogenéticos influencian cada vez más los cuestionamientos sobre la taxonomía de las subespecies. Varios ejemplos recientes destacan la necesidad de un abordaje filosófico claro y consistente de como los datos genéticos son usados para determinar los límites de las subespecies (Patten, 2015).

La confusión del significado y uso del concepto subespecie surgió en los primeros años de la taxonomía, principalmente porque algunos investigadores utilizaban la palabra para referirse a variaciones geográficas de una especie, por lo tanto cualquier población natural distinta que no se considerara suficientemente diferente para ser reconocida como una nueva especie, era catalogada como una subespecie (Mayr, 1982). En el caso de la distribución continental de *Eira barbara*, las poblaciones con distintas variaciones fenotípicas colindan unas con otras y no están geográficamente separadas entre sí, no hay motivos para pensar que no existe flujo génico entre poblaciones contiguas, esta asunción está respaldada por los resultados de Ruiz-García *et al*., (2013), los cuales indican que en Sudamérica existen dos poblaciones genéticamente diferentes de *Eira barbara*.

La subcategoría taxonómica de subespecie tiene limitaciones en su concepción y uso, debe considerarse que el concepto se originó cuando los principios de la taxonomía estaban en formación, su implementación ha sido útil en diversas investigaciones pero también resulta problemática en muchas otras. Los avances en genética actualmente permiten identificar diferencias moleculares entre organismos de una misma especie, la decisión de clasificar estos organismos en una categoría inferior a la de especie debe tomarse con cautela ya que el concepto de subespecie actualmente está rebasado.

Hábitos

Eira barbara es de hábitos solitarios, diurno, con picos de actividad durante los periodos crepusculares, se desplaza dentro de un rango de distribución extenso, pasa gran parte del día forrajeando o descansando en árboles (Sunquist *et al.* 1989). Se desplaza sin inconvenientes en suelo, árboles y ramas horizontales, utiliza su cola para mantener el equilibrio (Kaufmann & Kaufmann, 1965).

En vida libre pueden encontrarse solos (Osgood, 1912, 1914, 1916; Galef *et al.* 1976; Defler, 1980; Emmons & Freer, 1990) o en parejas de macho y hembra (Dalquest, 1963; Kaufmann & Kaufmann, 1965; *Galef et al.* 1976; Defler, 1980; Konecny, 1989), lo cual solo ocurre durante la época reproductiva (Aquino *et al.* 2001). Los grupos grandes (más de tres individuos) de *Eira barbara* por lo general están integrados por una hembra con sus crías subadultas (Dalquest, 1953; Leopold, 1959, Aquino *et al.* 2001).

Dieta

Son cazadores activos que persiguen a sus presas, utilizan el olfato como el método principal para detectarlas, teóricamente su sentido de la vista es relativamente pobre (Defler, 1980). Algunos investigadores afirman que *Eira barbara*, se alimenta de frutos, invertebrados y pequeños vertebrados como aves y roedores (Aquino *et al*. 2001). También es descrito como un omnívoro oportunista que consume una gran variedad de frutos, carroña, pequeños vertebrados, insectos y miel (Cabrera & Yepes, 1960; Hall & Dalquest, 1963; Galef *et al.* 1976; Emmons & Freer, 1990, Presley, 2000).

Debido a la dificultad para obtener excrementos de *Eira barbara* de vida libre, no se ha analizado su dieta. Teoricamente la especie podría desarrollar un papel clave en los ecosistemas donde no hay presencia de grandes depredadores, al controlar las poblaciones de mamíferos pequeños y medianos (Lindenmayer, 1999; Camargo & Ferrari, 2007).

Figura I-3. Vista lateral y ventral del cráneo de *Eira barbara*. La fórmula dental de un ejemplar adulto es: I 3/3, 1/1 C, P 3 / 3-4, M 1 / 1-2 (total 34 dientes); Presley (2000).

Reproducción y cuidado parental

De acuerdo con las investigaciones de Vaughan (1974) y Poglayen-Neuwall (1975) los machos son reproductivamente viables a partir de los 18 meses de edad, las hembras tienen su primer ciclo estral alrededor de los 22 meses de edad, son poliéstricas durante el año por períodos de 3-20 días. La gestación dura entre 63 y 67 días, luego de los cuales nacen entre una y tres crías, los machos no permanecen junto a las hembras y crías (Presley, 2000).

Cuando las crías nacen están cubiertas de pelo, pesan aproximadamente 100 gramos, sus orejas se abren entre los 27 a 34 días y los ojos a los 35 a los 47 días, los dientes de leche comienzan a emerger a los 36 días y alcanzan su desarrollo definitivo al día 99. Las piezas permanentes aparecen en el día 115 y están completamente desarrolladas al día 224 (Poglayen-Neuwall, 1978), las crías consumen comida sólida a los 70 días y son destetados a los 100 días, alcanzan el tamaño adulto a los seis meses y es difícil diferenciarlos de sus padres (Encke, 1968).

La madre utiliza una vocalización para comunicarse con las crías, el llamado está basado en chasquidos (en inglés es nombrado *clicking call*; Presley, 2000). La habilidad de capturar y matar presas se aprende y desarrolla lentamente (Poglayen-Neuwall & Poglayen-Neuwall, 1976), a los tres meses de edad las crías reciben animales heridos por parte de la madre, a través de la experiencia, las crías aprenden a posicionar la mordida en la base del cráneo de la presa, de esa forma adquieren la capacidad de cazar y matar (Poglayen-Neuwall & Poglayen-Neuwall, 1976).

Referente al crecimiento de las crías, Poglayen-Neuwall & Poglayen-Neuwall (1976) describen cinco estados de desarrollo:

1) El estado de infante (entre 1 y 50 días), durante el cual las crías lactan y no dejan la madriguera. 2) Entre los 50 a 75 días, las crías dejan la madriguera por cortos períodos y se alimentan de comida sólida provista por la madre en adición a la leche. 3) El destete, incluye excursiones exploratorias con alimentación independiente, consumen frutas e insectos. 4) Durante el estado de transición, entre los 100-200 días, las madrigueras son abandonadas, los jóvenes empiezan a cazar con su madre y matar sus propias presas. 5) Durante la dispersión, entre los días 200 a 300, la familia se desintegra y el ejemplar joven toma un camino separado.

Registros en vida libre y en cautiverio

Por lo general los registros más recientes de *Eira barbara*, corresponden a resultados colaterales de investigaciones enfocadas al estudio de otras especies; o avistamientos esporádicos; en esos casos los reportes señalan su presencia en la región. Los registros obtenidos han sido utilizados en notas científicas, artículos de divulgación e investigaciones enfocadas en la diversidad faunística de determinados ecosistemas.

En México *Eira barbara* ha sido registrada mediante el uso de cámaras trampa en los estados de Hidalgo (Morales-García *et al.* 2016), Querétaro (López-González & Aceves-Lara, 2007), Puebla (Ramírez-Bravo, 2011), Guerrero (Ruiz-Gutiérrez, Vázquez-Arroyo, & Chávez, 2017), Oaxaca (Pérez-Irineo & Santos-Moreno, 2012; Espinosa-Lucas *et al.* 2015; Peña Azcona, Gómez Ugalde, & Briones-Salas, 2015), Veracruz (Rodríguez-Macedo, González-Christen, & León-Paniagua, 2014), Chiapas (Monterrubio, Lara, Piñera, & Torres, 2005; Vaca-León, 2014) y Campeche (Briceño *et al.* 2017; Hidalgo-Mihart *et al.* 2017). Los registros fueron obtenidos en diferentes tipos de vegetación y diferentes gradientes altitudinales.

La especie ha sido registrada en diferentes ecosistemas de Centro y Suramérica (Tabla I-1). La mayor cantidad de investigaciones han sido desarrolladas en Brasil, en donde se han reportado variaciones no comunes en la coloración del pelaje (el cual es blanco amarillento en todo el cuerpo) de *Eira barbara* (Tortato & Althoff, 2007; Venturini *et al.* 2016) y algunos casos de leucismo (Talamoni *et al.* 2017).

Tabla I-1. Investigaciones científicas del Continente Americano que reportan la presencia de *Eira barbara*.

País	Autores, año
Guatemala	Escobar-Anleu *et al.* 2017
Costa Rica	González-Maya *et al.* 2015
Colombia	Parra-Colorado *et al.* 2014; Mosquera-Muñoz, *et al.* 2015; Quintana-Diosa, *et al.* 2016.
Ecuador	Reyes-Puig *et al.* 2015; Hidalgo, 2016; Hodge & Arbogast, 2016; Lizcano *et al.* 2016.
Perú	Espinosa *et al.* 2016; Torres-Oyarce *et al.* 2017.
Brasil	Camargo & Ferarri, 2005; Gumier-Costa & Sperber, 2009; Campos & Mourão, 2015; Fernandes-Ferreira *et al.* 2015; Martins *et al.* 2015; Timo *et al.* 2015; Aximoff & Rosa, 2016; Campos *et al.* 2016; Massara *et al.* 2016; Santos *et al.* 2016; Ferreguetti *et al.* 2017; Guerra & Leite, 2017; Luna *et al.* 2017; Regolin *et al.* 2017; Abra, *et al.* 2018.
Argentina	Albanesi *et al.* 2017.

Se asume que las poblaciones de *Eira barbara* están disminuyendo, no existen investigaciones que corroboren o refuten estas afirmaciones. Teóricamente su principal amenaza consiste en la pérdida de hábitat por destrucción de los bosques (Cuarón, 2008). No se le atribuyen depredadores.

Como un esfuerzo inicial para generar información ecológica que sirva de base para futuros estudios de *Eira barbara,* se realizaron dos investigaciones diferentes con el objetivo de contribuir al conocimiento que se tiene sobre la especie. La información se divide en capítulos que abordan diferentes aspectos ecológicos de la especie:

Capítulo 1: Throat Patch Variation in Tayra (*Eira barbara*) and The Potential for Individual Identification in the Field.

Capítulo 2: Activity patterns of tayra (*Eira barbara*) across their distribution.

Capítulo 1.
Throat Patch Variation in Tayra (*Eira barbara*) and the Potential for Individual Identification in the Field

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Abstract: The importance of identifying individuals of a population has been extensively documented in several species of carnivores, including some species of mustelids. This information is used in many kinds of ecological studies including density estimation, behavioral ecology and analyses of animal movement patterns. The objective of the present study was to determine if individual variation in the throat patches of Tayra (*Eira barbara)* permits individual identification. We examined 275 specimens from museum collections to determine the morphological variation of the throat patch in *Eira barbara* specimens collected throughout its distribution. We found differences in the shape and size of the throat patches significant enough to allow discrimination of individuals that display a throat patch (88.0% of 252 complete specimens). The proposed identification criterion was applied to photographic records obtained from a wild population using camera traps in the Peruvian Amazon. From nineteen images (54.0% of all images) in which the throat patch was visible, nine different individuals were identified and two of these were recaptured on multiple occasions.

Keywords: Camera traps; Carnivora; neotropical; Mustelidae; Non-invasive survey; Peruvian Amazon.

1.1. Introduction

Individual identification of free-living animals allows one to differentiate among individuals of a species and estimate the size of its population. One of the most commonly used procedures is the capture-recapture of individuals based on the Lincoln-Petersen method (González-Romero, 2011). In a first sample, animals are captured, marked and released, and subsequently another sample of the population is captured. The proportion of individuals marked in the second sample permits the estimation of the total population size (Páez & Lezama, 1998). This basic model form was expanded to allow testing of various hypotheses about the factors influencing capture probability (Otis *et al.* 1998) and more recently to allow the incorporation of spatial information (Borchers & Efford, 2008) yet the need for "capture" remains in all cases. Physical capture (and recapture) of individuals is not only invasive and potentially dangerous, but can be challenging or impossible in the case of many large and/or elusive mammals (Kirkland, 1998). Fortunately non-invasive approaches exist for "capture" and "marking" of animals, and photo-identification, often through the use of motion/heat activated trail cameras, has been widely used in a capture-mark-recapture context to estimate population sizes (Testé & Denis 2013; Burton *et al*. 2015).

From photographic records, it is sometimes possible to characterize specific phenotypic patterns in an individual animal. In the case of mammals, some species have spots, rosettes or stripes on the coat, which are unique features and do not change with time (Hammond *et al*. 1990; Harmsen *et al*. 2017). As a result, photographic records can represent marking events, with subsequent photos representing recaptures. These photo records can then be analyzed to determine the number of different individuals of a species that were not only photographed but also missed. The information obtained from the individual identification of animals is essential in the study of animal behavior and population demographics (Harrison, 2016).

There are examples in the literature of individual identification of wild mustelids (Carnivora: Mustelidae). Trujillo *et al*. (2008) described individuals of the giant otter (*Pteronura brasiliensis*) with a uniquely patterned white-yellow chest patch. Magoun *et al*. (2008) identified individuals of wolverine (*Gulo gulo*) through the observation of the unique light-colored patterns on the chest, throat, and chin area. Sirén *et al*. (2016) recognized and contrasted individuals of American marten (*Martes americana*) through the analysis of the ventral patch on the chest and throat. Harrison (2016) analyzed the pattern of the dorsal head stripes of the American badger (*Taxidea taxus*), identified individuals in the wild, and subsequently verified the difference of these characters among preserved individuals in a zoological collection.

The tayra (*Eira barbara*) is a neotropical scansorial (with terrestrial and arboreal habits) mustelid with a distribution that extends from the coasts of Central Mexico to northern Argentina (Figure A1). This species has variable coat color across its distribution that ranges from uniform (Figure 1-1a) to disruptive (Figure 1-1b). Seven subspecies based on coat - coloration variation have been recognized throughout its range; three for Mexico to Panama, and the rest for South America (Table 1-1; Hall, 1981; Presley, 2000). Recent research based on analysis of mitochondrial DNA has reduced the number of subspecies in South America from five to two (Ruiz-García *et al.* 2013). The exact number of subspecies remains questionable with their current geographical distribution and the status of their populations unknown.

(**a**) (**b**)

Figure 1-1. (**a**) Specimen of *Eira barbara* with uniform coloration (Nick Hawkins®); (**b**) Specimen with disruptive coloration (Villafañe-Trujillo®).

Eira barbara has been little studied and current records of the species include sightings, footprints and/or photographs through camera trapping, but are collateral results of research focused on other species (Camargo & Ferrari, 2007; Morales García *et al*. 2016).

Methods to identify individuals of *E. barbara* have yet to be reported. To date the identification of a specimen through photographic capture has only related to sex, provided the genitals of the organism are observed (e.g., Ramírez Bravo, 2011). The identification at the individual level using the phenotypic characteristics of *Eira barbara* is complicated. The color of the pelage of the head, neck, trunk, limbs, and tail is very similar, although in some geographic areas the tonality of the hair of the head and neck is different to the rest of the body. However, most populations of *E. barbara* have a distinct throat patch (Table 1-1), similar to that reported for other mustelids, where the feature has been successfully used for individual identification (Trujillo *et al*. 2008; Sirén *et al*. 2016). To date it has not been demonstrated whether throat patch variation in *Eira barbara* may allow discrimination between individuals, and whether the utility of the throat patch for this purpose varies geographically across the species' range.

Table 1-1. Names and descriptions of the seven subspecies of *Eira barbara* recognized by Cabrera (1958) and Hall (1981); compiled by Presley (2000).

Subspecies	**Coloration**				**Presence of Throat Patch**	**Observations**	**Distribution ****
	Body	**Legs**	**Nape**	**Head**			
barbara [1]	Dull brown	*	*	No distinct gray to brown	Yes, yellowish	Body is lighter than *E. b. sinuensis* and darker than *E. b. senex*	Paraguay, part of Brazil, Peru, Bolivia, and Argentina
sinuensis [2]	Black	*	Darker brown than the head.	*	May be present	Body is darker than *E. b. senex*	Panama, part of Costa Rica, Venezuela, Colombia, and Ecuador
poliocephala [3]	Dull brown	*	*	Brown	Yes, yellowish	Pelage is similar to that of *E. b. barbara* but with a darker yellow throat patch and yellow shoulder patches, which sometimes join forming a complete yellow collar	Guyana, French Guyana, Surinam, part of Brazil and Venezuela
peruana [4]	Dark chocolate brown	Darker than body	*	*	*	The color of the body is as in *E. b. madeirensis*, except that limb, are darker than body and tail is black	Part of Peru and Bolivia
senex [5]	Dark brown		Grayish white		Yes, yellowish	The grayish white color extends to shoulders fading to a dark yellow	Belize, part of Mexico, Guatemala, and Honduras
inserta [6]	Black	*	*	Dark brown	No	*	El Salvador, Nicaragua, part of Guatemala, Honduras and Costa Rica
madeirensis [7]	Dark chocolate brown	*	Slightly lighter than body		May be present	*	Part of Brazil, Venezuela, Colombia, Peru, and Ecuador

* = The original authors did not detail the description of the subspecies; ** = It represents an approximate distribution of the subspecies, obtained from maps generated by Cabrera (Cabrera, A., 1958) and Hall (Hall, E. R., 1981); The subspecies are organized as described by different authors: [1] = Linnaeus, 1758; [2] = Humboldt, 1812; [3] = Traill, 1821; [4] = Nehring, 1886; [5] = Thomas, 1900; [6] = Allen, 1908 and [7] = Lunnberg, 1913.

The objective of the present study was to characterize the morphological variability of the throat patch of different museum specimens of *Eira barbara* collected throughout its range to determine if the throat patch character allows for the identification of individuals of this species. In addition, we aimed to investigate the applicability of our findings in a field setting, by attempting to identify individuals from camera trap photos collected in the Peruvian Amazon.

1.2. Materials and Methods

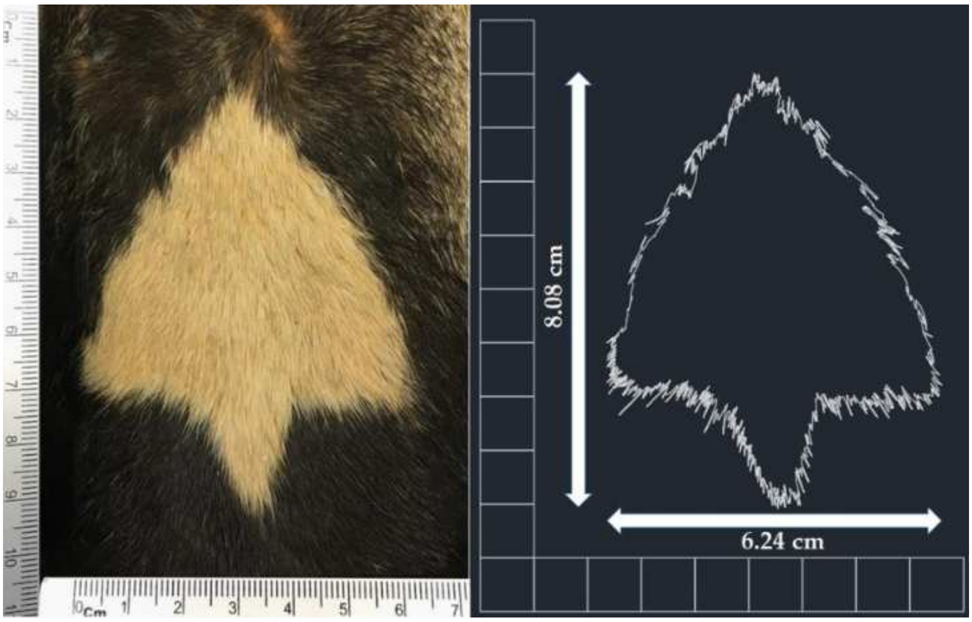
We made a review of the zoological collections of the American continent that could contain specimens of *Eira barbara*, and we contacted the curators to request permission to access their collections. Subsequently we visited the collections that had the largest number of specimens, and the Mexican collections that granted their authorization to examine the specimens. We recorded the collection information available for each specimen, and grouped each specimen by country of collection.

We photographed the throat patch of each of the specimens at a consistent distance (10 cm; Figure 1-2a), with a ruler visible to allow setting of the correct scale in the photographs taken. We analyzed the images using AutoCAD software (version 2016), in which the outline of each throat patch was delineated. To identify the length of the patch we measured the distance between the top vertical vertex and the lower vertical side, we obtained the width of each throat patch by measuring the maximum distance between the opposing horizontal vertices (Figure 1-2b). Finally, we obtained the area and perimeter of each patch.

Because shape is a difficult parameter to quantify concisely in a metric (McGarigal & Marks, 1994), we used a Shape Index to characterize throat patch shapes, with calculations based on the relationship between the area and perimeter of a polygon, which facilitates the understanding of a factor at the morphological and functional level (Vila Subirós *et al*. 2006). We used the modification of the Patton's Index (1975) made by McGarigal and Marks (1994) using the formula:

$$\text{Shape} = p_i/2\sqrt{\pi \cdot a_i}$$

where p_i is the perimeter (m) of the patch i, and a_i is the area (m^2) of the patch i, the formula can be read as: shape equals patch perimeter (m) divided by the square root of patch area (m^2), adjusted by a constant to adjust for a circular standard. Thus, although patches may possess very different shapes, they may have identical areas and perimeters and shape indexes. For this reason, this shape index is best considered as a measure of overall shape complexity that compares the complexity of a patch shape to a standard shape. In the vector version of FRAGSTATS (version 2.0, McGarigal & Marks, 1994), patch shape is evaluated with a circular standard, with the index referenced as a minimum (1) for circular patches and increasing as patches become increasingly noncircular (McGarigal & Marks, 1994).



(**a**) (**b**)

Figure 1-2. (**a**) Original photograph; and (**b**) Digitized contour of the throat patch from a museum specimen of *Eira barbara*.

A Wild Population Case Study

To determine the usefulness of potential identification criteria in wild populations, we analyzed independent photographic events of *Eira barbara* obtained in the Peruvian Amazon between April and September of 2008. These photographs were the product of a survey designed to estimate density of *Leopardus pardalis* (Kolowski & Alonso, 2010) in which 23 camera stations were established, each with two Reconyx RC-55 (Holmern, WI, USA) digital infrared trail cameras placed in lowland tropical rainforest. The sampling effort was of 3068 camera-nights, and the stations formed a polygon of 22 km^2. Cameras were set to take three photos per trigger on the "rapidfire" setting, which allows approximately one photo to be taken per second. The photographs obtained from *Eira barbara* separated by 24-h cycles were considered as independent events. Photographs were reviewed in which the position of the organism allowed observation of the throat patch and the images were grouped according to the angle of observation: (a) frontal catches, (b) left side capture and (c) right side capture. Individual identification was attempted for all photographs showing any angle of the throat patch, yet additional characteristics including the presence of testes, ear shape, and overall coat coloration were used to confirm identifications when necessary.

1.3. Results

A total of 275 museum specimens of *Eira barbara* were available for examination; 15 specimens belonged to six zoological collections of Mexico, 103 records belonged to the Division of Mammals of the National Museum of Natural History of the Smithsonian Institution, and 157 specimens were from the zoological collection of the American Museum of Natural History of the United States (Table 1-2).

Table 1-2. Reviewed Zoological Collections and number of specimens of *Eira barbara* examined, including details about the status of reviewed specimens.

Country	Collections	Number of Specimens	Specimens with Throat Patch	Specimens without Throat Patch	Analyzed Throat Patch	Incomplete Specimens **
Mexico	Colección Nacional de Mamíferos (CNMA).	2	2	0	2	0
	Colección Mastozoológica del Zoológico Miguel Álvarez del Toro (ZOOMAT).	3	3	0	3	0
	Colección de Mamíferos del Instituto de Investigaciones Biológicas de la Universidad Veracruzana (IBB-UV).	1	1	0	1	0
	Laboratorio de Mastozoología de la División Académica de Ciencias Biológicas de la Universidad Juárez Autónoma de Tabasco (DACBIOL-UJAT).	1	1 *	0	0	0
	Colección Mastozoológica de El Colegio de la Frontera Sur (ECOSUR).	4	4	0	4	0
	Colección Mastozoológica del Centro de Estudios en Desarrollo Sustentable y Aprovechamiento de la Vida Silvestre de la Universidad Autónoma de Campeche (CEDESU-UAC).	4	3	1	3	0
United States	The Division of Mammals of the National Museum of Natural History (NMNH), Smithsonian Institution.	103	74	14	24	15
	Mammalogy Collection of the American Museum of Natural History (AMNH).	157	133	15	36	8
Total		275	222	30	73	23

* = The characteristics of the specimen did not allow analysis of the form of the throat patch; ** = The skin of the specimen is incomplete and/or the gular area is absent.

The records of the 275 specimens of *Eira barbara* were grouped from the country where they were collected; ten records from Zoo specimens (unknown origin) were grouped in the category named Zoo. Among the analyzed specimens, we found eight specimens whose phenotypic characteristics do not match the description of any taxonomic group currently recognized; these specimens have a white or yellow pelage over all the body with a black snout. They were not included in our detailed analysis because two specimens had a stitched throat patch, and of the remaining six specimens, three had no throat patch and three others were incomplete. The specimens studied were classified into different categories (Figure 1-3).

Figure 1-3. Type of specimens found in different Zoological Collections. (**a**) Specimens with entire throat patch (n = 73); (**b**) Specimen with entire throat patch that extends through neck, shoulder and back (n = 8); (**c**) Specimen with entire throat patch obscured (n = 8); (**d**) Specimen with throat patch cut during preservation (n = 83); (**e**) Specimen with stitched throat patch (n = 27); (**f**) Specimen with incomplete throat patch (n = 23); (**g**) Specimens without throat patch (n = 30); and, (**h**) Incomplete specimens (n = 23).

Of the 275 specimens examined, 222 specimens of *Eira barbara* had a throat patch yet only 81 patches were complete. Eight of these 81 samples were excluded because the throat patch extended through the neck, shoulder and back; in these cases the throat patches did not have a limit (Figure 1-3b) and were impossible to measure. Therefore, only 73 throat patches were used to characterize morphological measurements and the shape index (Table 1-3, Table A1).

Table 1-3. Country of origin (in latitudinal order, north to south) of the specimens of *Eira barbara* examined in the Zoological Collections and their throat patch status.

Country	Specimens with Throat Patch	Specimens without Throat Patch	Incomplete Specimens	Total	Number of Measured Throat Patches
Mexico	25	5	1	31	17
Guatemala	7	0	0	7	4
Honduras	2	0	0	2	2
El Salvador	1	0	0	1	0
Nicaragua	3 *	5	1	9	0
Costa Rica	9	4	0	13	4
Panama	20	9	13	42	8
Colombia	34	0	1	35	15
Venezuela	17	4	0	21	4
Trinidad and Tobago	1	0	0	1	1
Guyana	13	3	3	19	1
Brazil	27	0	0	27	6
Ecuador	15	0	2	17	4
Peru	27	0	0	27	2
Bolivia	11	0	0	11	2
Paraguay	1	0	0	1	1
Argentina	1	0	0	1	1
Zoo **	8	0	2	10	1
Total	222	30	23	275	73

* = Throat patches cut during preservation; ** = Specimens of unknown geographical origin.

The contours of the throat patches examined were an irregular polygon form, which differed in the number of sides and vertices that composed them. As a result, all the throat patches lacked an axis of symmetry.

The morphological measurements of the 73 throat patches differed in the length, width, area, and perimeter that occupy each patch. The length values ranged from 0.96 to 14.70 cm (throat patches S50 and S27 respectively, Table A1) with a mean length of (6.03 ± 3.03 cm). The average width of the 73 analyzed patches was (4.31 ± 1.98 cm) with the values ranging from 0.58 to 8.38 cm (patches A1 and S17 respectively, Table A1). There was a significant positive correlation ($p = 0.76$) between the length and width values of the 73 patches (Figure 1-4).

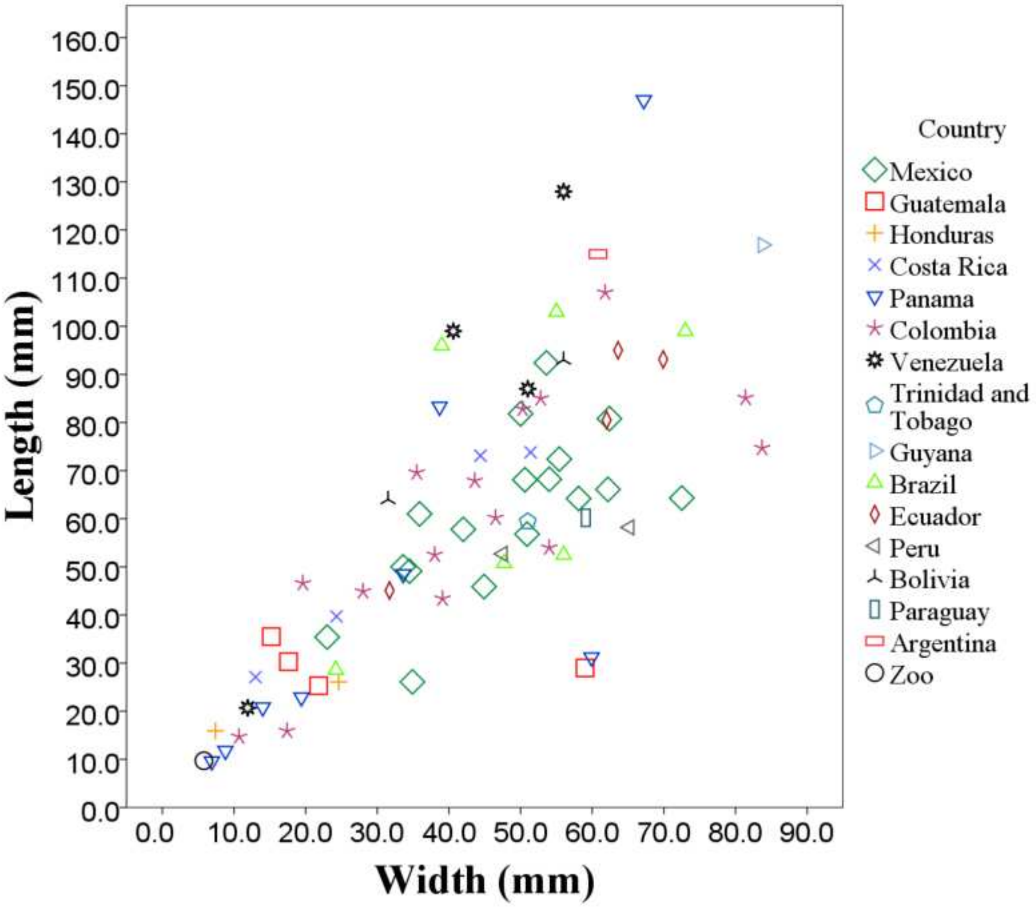


Figure 1-4. Dispersion of the values of length and width of the 73 throat patches examined of *Eira barbara*. $y = 1.04 + 1.16 \times x$.

The area of the throat patches varied between 0.15 cm^2 and 49.90 cm^2 (A1 and S27 respectively, Table A1) with an average area of (13.76 ± 11.18 cm^2). The perimeter values ranged from 9.28 to 441.98 cm (patches A1 and A2, Table A1) and the average was (143.14 ± 92.41 cm).

Analyzing morphological measurements of throat patches of specimens grouped by country of origin, the averages of the measures indicated that the longest throat patches belonged to specimens collected in Venezuela (8.36 ± 4.53 cm) and the smallest to specimens collected in Honduras (2.10 ± 0.72 cm). This situation was repeated with the measures of perimeter (205.63 ± 118.73 cm and 29.15 ± 21.93 cm respectively). The patches with the largest values of width and area corresponded to specimens collected in Ecuador (5.68 ± 1.70 cm and 21.80 ± 11.54 cm^2 respectively) and the smallest corresponded to specimens collected in Honduras, (1.60 ± 1.21 cm and 1.22 ± 0.98 cm^2 respectively, Table 1-4).

When plotting the values of the morphological measurements of the throat patches grouped by country of origin, geographic variation in the values of length, width, area and perimeter are evident (Figures 1-5, 1-6, 1-7, and 1–8). These data, taken along with clear differences in patch shape demonstrate large amounts of variation in patch characteristics both within and among countries. (Figure A2).

The 73 values of the shape index ranged from 5.29 to 20.70 (minimum and maximum respectively, Table A1), indicating that the throat patches have an irregular non-circular shape (Figure 1-9).

Table 1-4. Values of the morphological measurements of 73 throat patches of *Eira barbara* collected in different countries. Highest and lowest values in each column are shown in bold.

Country of Origin	Mean Length (cm)	Mean Width (cm)	Mean Area (cm^2)	Mean Perimeter (cm)
Mexico (n = 17)	6.12 ± 1.67	4.81 ± 1.28	14.70 ± 6.82	133.40 ± 50.16
Guatemala (n = 4)	3.00 ± 0.42	2.84 ± 2.05	4.23 ± 4.06	51.71 ± 31.11
Honduras (n = 2)	**2.10 ± 0.72**	**1.60 ± 1.21**	**1.22 ± 0.98**	**29.15 ± 21.93**
Costa Rica (n = 4)	5.34 ± 2.36	3.32 ± 1.77	7.89 ± 7.27	103.29 ± 70.43
Panama (n = 8)	4.68 ± 4.70	3.10 ± 2.30	9.50 ± 16.67	90.26 ± 70.61
Colombia (n = 15)	6.02 ± 2.55	4.41 ± 2.12	13.49 ± 10.59	149.86 ± 90.77
Venezuela (n = 4)	**8.36 ± 4.53**	3.98 ± 1.97	17.37 ± 11.15	**205.63 ± 118.73**
Trinidad and Tobago (n = 1)	5.94 *	5.10 *	16.19 *	79.25 *
Guyana (n = 1)	11.69 *	8.38 *	45.91 *	307.26 *
Brazil (n = 6)	7.16 ± 3.15	4.91 ± 1.65	17.68 ± 10.48	203.50 ± 109.91
Ecuador (n = 4)	7.84 ± 2.31	**5.68 ± 1.70**	**21.80 ± 11.54**	183.73 ± 56.07
Peru (n = 2)	5.54 ± 0.38	5.63 ± 1.25	11.75 ± 0.75	155.38 ± 31.95
Bolivia (n = 2)	7.85 ± 2.05	4.37 ± 1.73	12.08 ± 8.71	172.12 ± 64.41
Paraguay (n = 1)	6.02 *	5.91 *	16.09 *	261.88 *
Argentina (n = 1)	11.50 *	6.08 *	36.30 *	441.98 *
Zoo (n = 1)	0.97 *	0.58 *	0.15 *	9.28 *

* The data correspond to a single specimen; the values do not have mean or standard deviation.

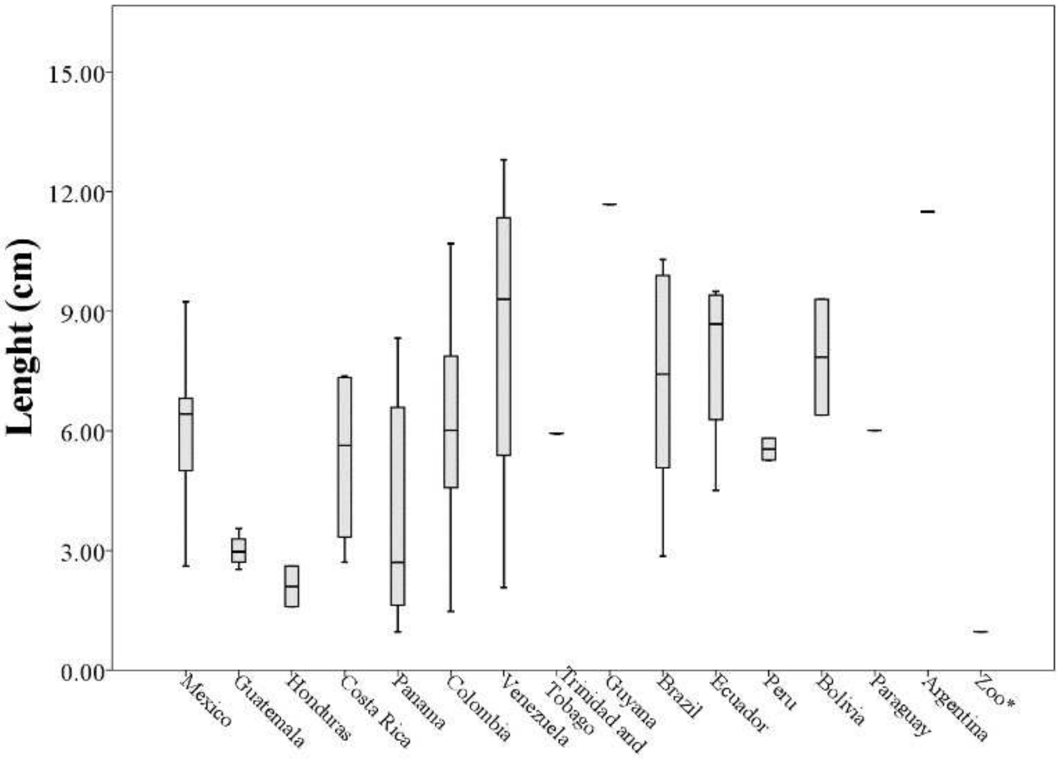


Figure 1-5. Variation of the length measures (cm) of the throats patches from 73 analyzed museum specimens of *Eira barbara*. * = Specimen of unknown geographical origin.

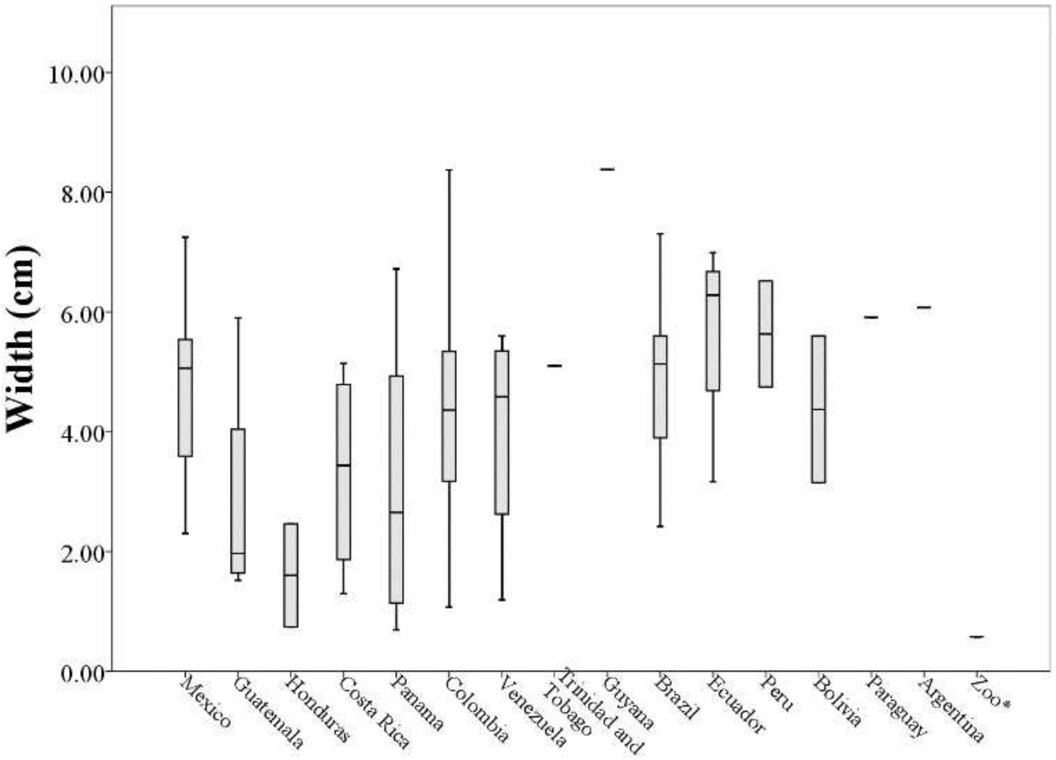


Figure 1-6. Variation of the width (cm) of the throats patches from 73 analyzed museum specimens of *Eira barbara*. * = Specimen of unknown geographical origin.

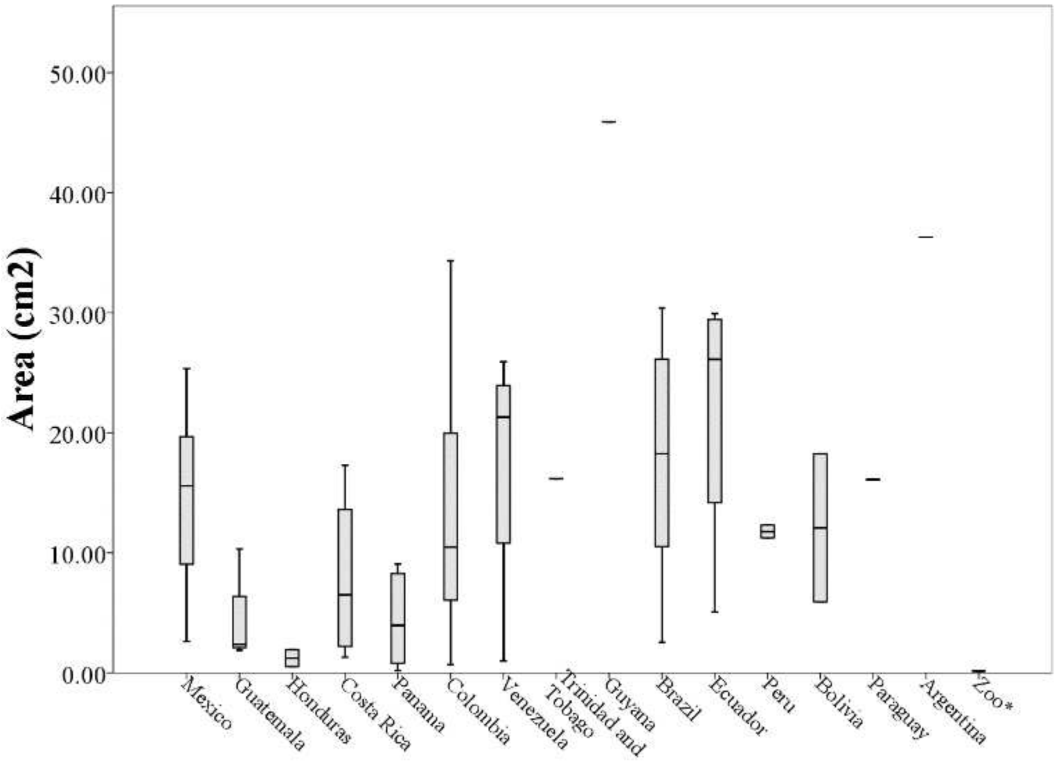


Figure 1-7. Variation of the area (cm²) of the throats patches from 73 analyzed museum specimens of *Eira barbara*.* = Specimen of unknown geographical origin.

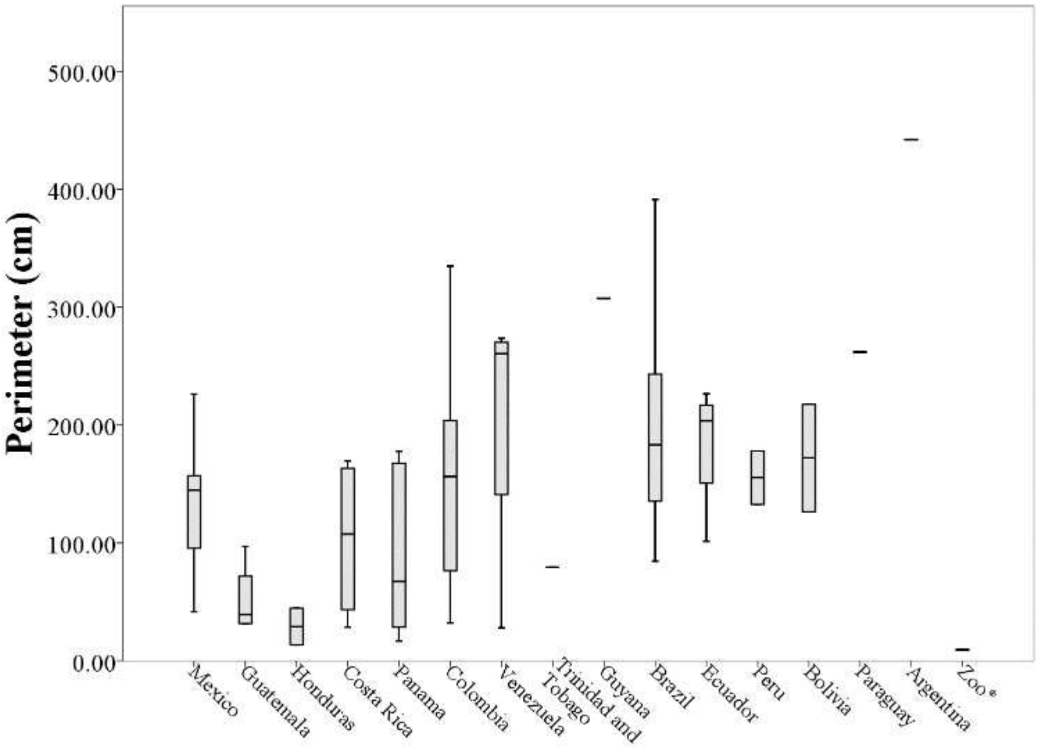


Figure 1-8. Variation of the perimeter (cm) of the throats patches from 73 analyzed museum specimens of *Eira barbara*. * = Specimen of unknown geographical origin.

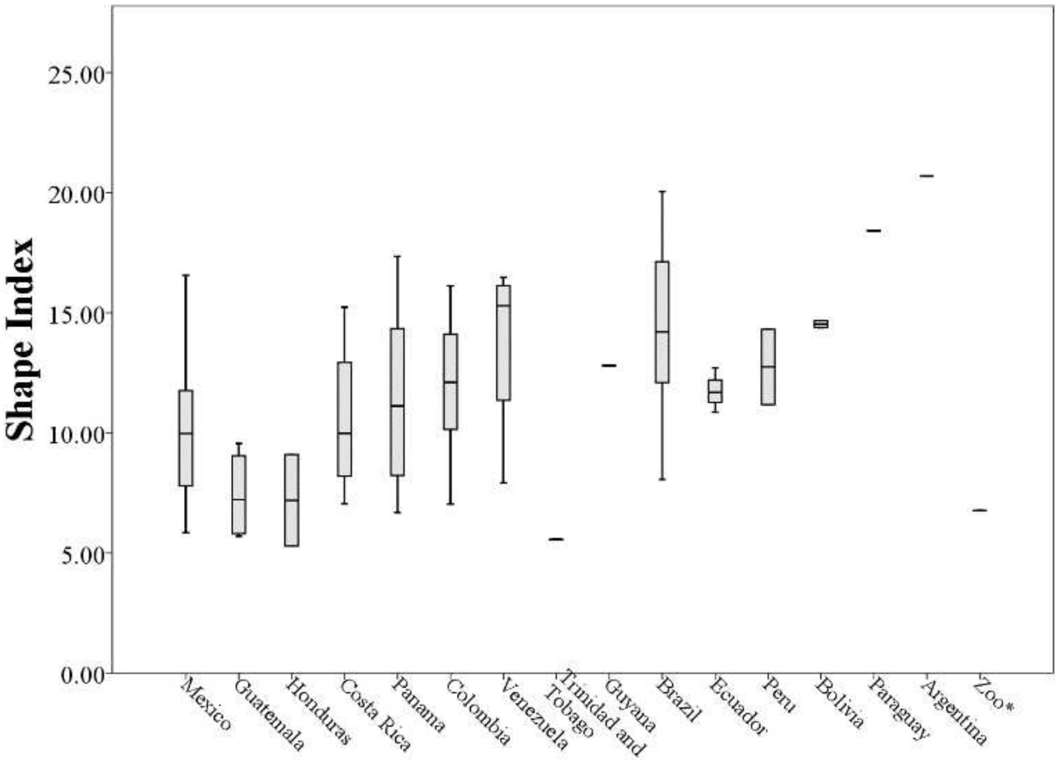


Figure 1-9. Variation of the shape index values of the throats patches from 73 analyzed museum specimens of *Eira barbara*. * = Specimen of unknown geographical origin.

A Wild Population Case Study

We registered 35 independent photographic events with *Eira barbara* in the Peruvian Amazon. In 19 events (54.0%) a clear image was obtained of the throat patch, which was subsequently used to identify individuals. For all 19 of these events, we were able to assign an individual to the event. In total, nine different individuals were identified: four males and five animals of indeterminate sex (Figure 1-10, Figure A3). Two individuals were photographed on different dates; individual B eight times and individual F four different times. Both of these individuals were recaptured only in the same camera-station. The other seven individuals were photographed only on a single occasion (Table 1-5). In two independent photographic events more than one individual was pictured; in one event two tayras were pictured and another included three in the same photograph.

Figure 1-10. Comparison of the throat patch of the nine (**a**–**i**) uniquely identifiable individuals. Note that both the frontal (**a**–**d**) and lateral images (**e**–**i**) can be used to differentiate among individuals.

In the photographs where the view is frontal (Figure 1-10, individuals a–d) it is observed that the contour and size (the space occupied by the patch in the gular area of the animal) of the four throat patches were different from each other. For the remaining individuals, only lateral views of the left (Figure 1-10, individuals e–g) or the right side (Figure 1-10, individuals h,i) were available and individual identification was still possible. However in some cases, particularly with individuals showing only lateral patch views, and where photo angles across different photo events were substantially different (e.g., Figure 1-10 e–g), additional characteristics, such as coat color variation and ear shape, were critical in confirming final identifications. Differential coat coloration between the neck and body was seen in 77.7% of the individuals (e.g., Figure 1-10e).

Table 1-5. Photographic events obtained of *Eira barbara* across 3068 camera-nights from 23 camera stations in the Peruvian Amazon in 2008. Also shown is the photographic capture record of the nine unique individuals identified from throat patch size, shape and location.

Observations	Months						Total
	April	**May**	**June**	**July**	**August**	**September**	
Number of independent photographic events	5	14	8	3	3	2	35
Capture events of males	1	10	5	2	1	1	20
Capture events of females	-	-	-	-	-	-	-
Capture events of unknown sex	5 *	4	5 *	1	2	1	18
Total capture events of tayras	6	14	10	3	3	2	38
Number of tayras without visible throat patch **	5	2	4	1	3	2	17
Number of tayras with visible throat patch	1	12	6	2	-	-	21
Number of identified tayras	1	12	4	2	-	-	19
Identified individuals							
a—unknown sex	-	1	-	-	-	-	1
b—male ***	-	6	1	1	-	-	8
c—unknown sex	-	-	1	-	-	-	1
d—male ***	-	-	1	-	-	-	1
e—unknown sex	-	1	-	-	-	-	1
f—male ***	-	2	1	1	-	-	4
g—unknown sex	-	1	-	-	-	-	1
h—unknown sex	1	-	-	-	-	-	1
i—male ***	-	1	-	-	-	-	1

* = An event included more than one tayra individual; ** = The throat patch is not observed because the photo took the back of the organism or the animal is far from the camera; *** = The penis and/or testicles of the individuals were observed.

Some museum specimens were not included in our detailed analysis because the throat patch were incomplete or artificially matched (i.e., stitched), and the coat color had particular characteristics which made them stand out from the others. In the case of the subspecies *Eira barbara poliocephala* the throat patch extends to the shoulders and back. In the specimens we examined it was evident that the form of this character also differs between organisms in this group (Figure 1-11a). It was observed that this character has an asymmetrical outline, and therefore has a different form in left and right lateral planes (Figure 1-11b).

Presley (Presley, 2000) pointed out that a yellow morph of *E. barbara* (Figure 1-12a) is relatively common in Guyana, and the eight specimens we found with this characteristics were all collected in Guyana. The throat patch was present in two of the eight examined specimens (Figure 1-12b), in the remaining six specimens, three had no throat patch (Figure 1-12c) and three others were incomplete.

(**a**) (**b**)

Figure 1-11. (**a**) Specimens of *E. b. poliocephala*, the throat patch extends through one or both shoulders. In the last two cases, the throat patches do not connect with the back patch; (**b**) Live specimen of *E. b. poliocephala* (Villafañe-Trujillo®), the throat patch extends through shoulders and back, the shape of the patch is different in each flank: right side (upper image) and left side (lower image).

(**a**) (**b**) (**c**)

Figure 1-12. (**a**) Specimen of *Eira barbara* with yellow and white pelage, record obtained in Guyana (Evi Paemelaere and Esteban Payan, Panthera®); (**b**) Yellow and white specimens, each one has a throat patch; (**c**) Yellow and white specimens without throat patches.

1.4. Discussion

Quantitative measurements of 73 throat patches have demonstrated that there is sufficient variation in the shape and size of each gular spot is unique in *Eira barbara*, this character can be used to identify tayras on an individual level. Analysis of camera trap photos from a Peruvian Amazon population has demonstrated that it is possible to individually identify tayras with this non-invasive method. The individual identification of tayras using the throat patch can be applied throughout the tayra range and for all the coat color variation in the species, including the white/yellow morphs and those with disruptive coat color.

The descriptions of the subspecies recognized by Cabrera (1958) and Hall (1981) reflect the phenotypic variability of *Eira barbara* through their geographical distribution. These descriptions are based on an arbitrary and subjective analysis of qualitative characters as opposed to genetic analysis. According to Avise and Ball (1990), the subspecies designation should be made based on concordant distributions of multiple independent (genetic) traits. Research conducted by Ruiz-García *et al*. (2013) was focused on generating a phylogenetic reconstruction between *Potos flavus* and *Eira barbara*. They analyzed biological samples of 68 specimens collected in South America and grouped them according to the five recognized subspecies in that region (*barbara*, *sinuensis*, *peruana*, *madeirensis* and *poliocephala*) according to Cabrera (1958) and Hall (1981). Molecular results suggest that in South America there are only two subspecies of *Eira barbara*: *barbara* (formed by groups *barbara*, *peruana*, *sinuensis* and *madeirensis*) and *poliocephala*. Consequently, the subspecies of *Eira barbara* currently recognized are four: *senex*, *inserta* (the result of phenotypic descriptions), *barbara* and *poliocephala* (the result of phylogenetic analysis).

Due to the lack of information concerning the coat color variation (regardless of patch characteristics) of *Eira barbara* throughout its area of distribution, we recommend a more comprehensive review of the available zoological collections of the world to generate detailed descriptions of the different existing phenotypes and maps of the distribution of each one. It is also necessary to perform the analysis of mitochondrial DNA of *mtCyt-b* and *mtNADH-5* of specimens collected in Central America with the aim of completing the investigation of Ruiz-García *et al*. (2013), and to identify if the populations of *Eira barbara* present from Mexico to Panama correspond to the subspecies distributed in South America (*Eira barbara barbara*) or if they comprise unique subspecies.

The specimens examined in this research were collected through almost all the area of distribution of the species, and 80.7% (222 of 275) of the examined specimens had a throat patch. However, 30 specimens (10.9%) examined did not have this character, and these were not melanic or albino organisms. Five (1.8%) were collected in Mexico, five in Nicaragua (1.8%), four in Costa Rica (1.4%), nine in Panama (3.2%), four in Venezuela (1.4%) and three in Guyana (1.0%). These results demonstrates that the absence of the throat patch is not restricted to a single population; this condition occurs throughout the northern half of the species range. Regardless, the presence of a clear throat patch in more than 80.0% of examined specimens indicates that this feature will typically be available for individual identification in field populations.

In the case of *Eira barbara,* the literature describes atypical coat coloration (Tortato & Althoff, 2007; Venturini *et al*. 2016). Krumbiegel (1942) argues that the cases of albinism and melanism are most common in *Eira barbara* than in any other species of mustelid. The lack of a throat patch may be a recurrent genetic mutation in the coloration of the coat similar to that taking place in melanism, albinism or leucism, which occurs in a small percentage of the population (Caro, 2005; Abreu *et al*. 2013). These genetic alterations have not been studied in *Eira*, but have been investigated in different mammalian species (Kettlewell, 1973; Elosegi *et al*. 2006; Morales García *et al*. 2016).

Some species of animals have some unique external characteristic which makes the identification of individuals feasible (Chehrsimin, 2015). The results of this research show that the form (geometric information that results from removing the effects of position, scale and rotation of an object, (Kendall, 1977)) and size of the patch on the throat is a distinctive character in every organism of *Eira barbara*. This feature serves as a point of individual reference that allows the identification and differentiation of organisms of *Eira barbara* that have a throat patch. Specific patterns in the coat of an animal are unique and do not change over time (Hammond *et al*. 1990). In the case of *Eira barbara,* theoretically, the size of the throat patch will increase proportionally until the animal reaches adult size (this occurs at six months of age, (Presley, 2000)).

Previous research that focused on the individual identification of mustelids (e.g., Magoun *et al*. 2008, Harrison, 2016; and Sirén *et al*. 2016) has been based on visual and subjective analysis of the obtained photographic records. Our research was based on the analysis of different quantitative and morphological characteristics of throat patches, which showed that the throat patch is a unique characteristic among individuals, and that it can be used as a basis for the individual identification of wild animals. Ours is the first to combine analysis of camera trap photos with quantitative measurements from a range of museum specimens across the species' range. This allows us to present conclusions on the potential feasibility of camera trap-based field studies throughout the tayra distribution.

A point in common our work and some previous investigations is that the individual identification is only possible when the photographic record of the animal is in a specific position, which allows detailed observation of the distinctive pattern in the pelage. In the case of *Gulo gulo* (Magoun *et al*. 2008) and *Martes americana* (Sirén *et al*. 2016) individual identification is only possible if the front of the gular area is photographed (ventral view), whereas in the case of *Taxidea taxus* (Harrison, 2016) it is only necessary to obtain photographs of any side of the head in lateral view. Our results for *Eira barbara* show that individual identification is possible with photographs showing the animal's gular area either with a front (ventral view) or side (lateral view). While a clear ventral view allows unambiguous identification from a single clear photograph, the lateral views require both sides to be photographed for unambiguous identification. In addition, the utility of lateral views is somewhat dependent on the angle of the photograph, and some body positions can obscure the throat patch to varying degrees. This is not the case with individuals of the subspecies *Eira barbara poliocephala*, where the throat patch extends over the shoulders and back, and where any lateral view will provide identifiable characteristics for that side. Field studies in Guyana, where the white/yellow morph appears to be common will face additional challenges where our limited sample size indicates the absence of a throat patch may be more common and throat patches, when present, may be more challenging to distinguish from camera trap photographs.

It could be difficult to differentiate individuals if only one side of the tayra is photographed. While it is possible to compare photographs of the same anatomical side of the animal, individual identification could be complicated when comparing different sides, as is the case with jaguars or other individually identifiable species (Silver *et al*. 2004). Given the non-symmetric forms of the patches, we would recommend that camera trap surveys aimed at estimating tayra populations include two cameras at each station as recommended for other species. In instances where only one camera per station is available, some additional options can improve the chances of unambiguous individual identification. First, the use of additional characteristics such as presence or absence of testicles, coat color variation, and shape of the ears, tail and body can certainly aid identification, and these factors were helpful in the identification of numerous individuals in our Peru field case study. Give this, camera setups that increase the amount of time the individual spends in front of the camera, and the chances that the animal will show clear views throat patch will improve one's ability to discriminate individuals with certainty. A range of commercial carnivore lures for example, are likely to at least slow the movement of this species and increase the number of angles from which the animal is photographed. In our field study, tayra reacted strongly to a proprietary carnivore lure (Weaver's Cat Call) and spent significant time investigated a scented stake placed in front of a subset of locations. Previous researchers have also designed custom bait stations which require individuals to expose their gular area to the camera while accessing the bait (e.g., Magoun *et al*. 2008; Sirén *et al*. 2016).

Newer spatially explicit capture-recapture (SECR) models designed to estimate density require a reasonable number of individuals to be captured on multiple occasions to allow unbiased estimation of capture probability (Royle *et al*. 2014). While there is no specific guidance on absolute lower thresholds, the nine individuals identified here is likely near the minimum number of individuals required for SECR models. Based on our field study and others, capture rates (independent photo events divided by sampling effort per 100 camera-nights) for tayra vary widely (this study: 1.14; Campeche, Mexico: 0.67 (Villafañe-Trujillo, unpublished data); Iguacu National Park, Brazil: 0.40 (Xavier da Silva *et al*. 2018) and are typically similar or below capture rates for jaguar in the same areas (this study, Tobler *et al*. 2008; Tobler *et al*. 2015). Estimation of jaguar densities using camera traps, while common, has been challenging to implement without bias due to low capture rates and large jaguar home ranges (Tobler & Powell, 2013). Given that capture rates of tayra are unlikely to be higher than those seen for jaguars, estimation of tayra density from camera surveys is likely to face similar challenges in accumulating enough individuals over a reasonably closed study period. Because our tayra capture rates appear to be at the higher end of those reported, our camera effort (3,068 camera-nights) should be seen as a minimum required to accrue sufficient tayra captures, and in some areas twice this value may be necessary. There is some indication that tayra may be more likely to be captured off trails (Tobler *et al*. 2015), and so future studies may consider this option to further increase capture rates. SECR studies also require that a large percentage of captured individuals be captured at multiple camera stations to allow estimation of an animal movement parameter (Royle *et al*. 2014). As a result, field studies aiming to use SECR to estimate density should aim for a camera spacing that attempts to find a compromise between maximizing the number of individuals captured (i.e. maximizing the size of the study area and capture probability), and maximizing spatial recaptures of individuals (i.e. minimizing camera spacing (Sollmann *et al*. 2012; Tobler & Powell, 2013; Royle *et al*. 2014). In this study, cameras were spaced on average 1.1 km apart, and none of the captured tayra were photographed at multiple camera stations, potentially suggesting that tayra in this region have relatively small ranges and that in general, spacing should be substantially less than 1km to ensure spatial recaptures of individuals.

1.5. Conclusions

This is the most comprehensive study of the coat morphology of this species to date. Throat patches were present in more than 80.0% of examined specimens (100% south of Peru). Using variation in morphological measurements and shape index values, we have demonstrated that the shape and size of every throat patch is a unique character in each specimen of *Eira barbara*. This information sets a precedent for the species, and demonstrates that the identification criteria presented here could be used to identify organisms of wild populations as in the cases of *Gulo gulo* (Magoun *et al*. 2008), *Martes americana* (Sirén *et al*. 2016) and *Taxidea taxus* (Harrison, 2016). The proposed identification criterion is applicable across the full distribution of *Eira barbara* and for all phenotypic variations described in the literature, and can be applied through non-invasive camera-based surveys to generate local population estimates for the species.

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Author Contributions: This study was co-designed and implemented by Álvaro José Villafañe-Trujillo as part of his Ph.D. thesis at the Universidad Autónoma de Querétaro, Mexico. Carlos Alberto López-González, his advisor, assisted with study design and manuscript writing. Joseph M. Kolowski designed and led the camera-trap design and field efforts during 2008, and assisted with manuscript writing.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

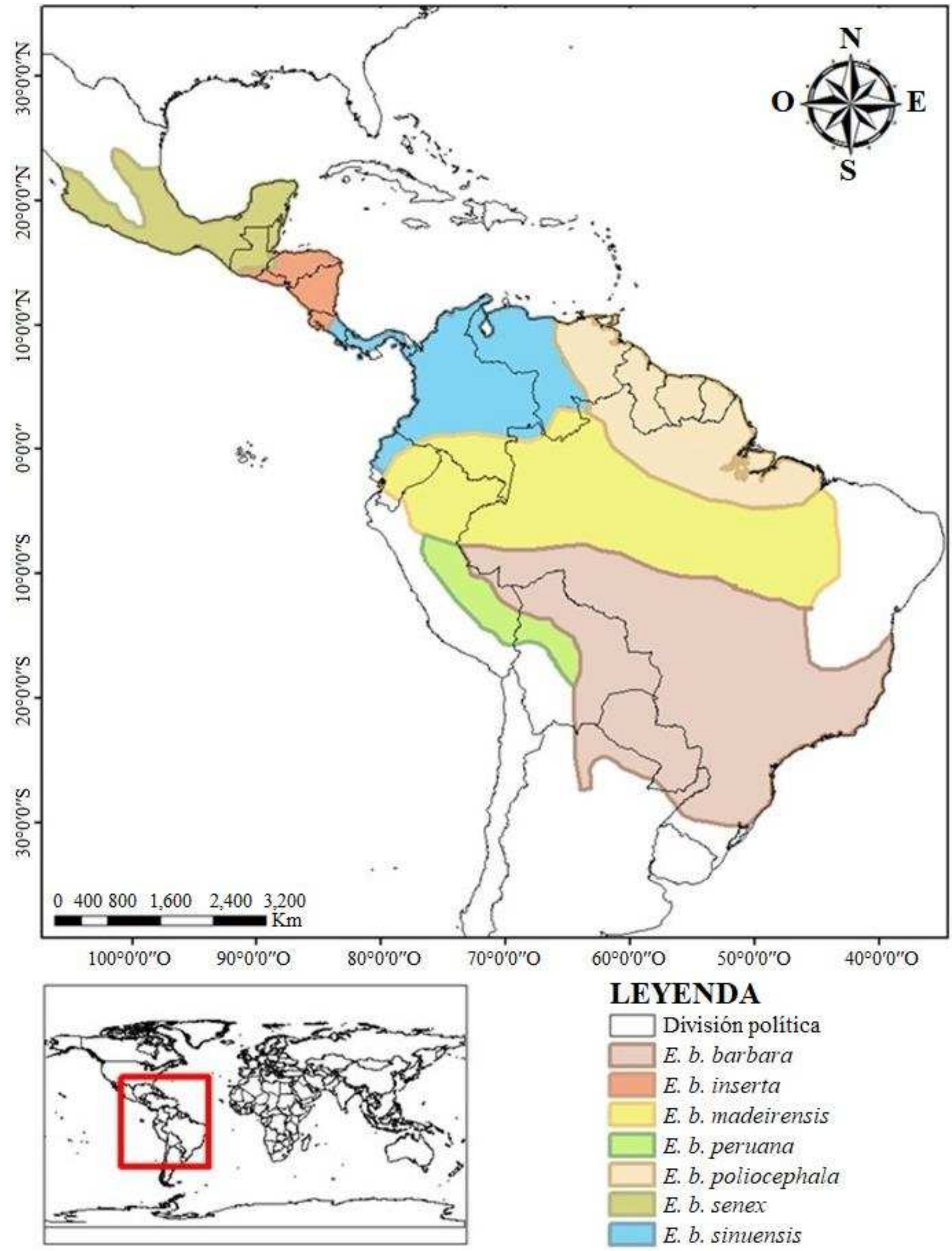

Figure A1: Geographic distribution of *Eira barbara*. The map corresponds to the data proposed by Cabrera 1958 and Hall 1981 (map modified from Presley (2000).

Appendix B

Table A1. Measures of the throat patches of 73 different museum specimens of *Eira barbara*.

Location	Name * of the Specimen in the Collection	Code	Length (cm)	Width (cm)	Area (cm^2)	Perimeter (cm)	Shape Index	Number in Collection
Zoo	Tayra barbara **	A1	0.97	0.58	0.15	9.28	6.76	6856/5516
Argentina	*Eira barbara barbara*	A2	11.5	6.08	36.3	441.98	20.70	185,325
Brazil	*Tayra barbara* **	A3	9.6	3.9	22.5	135.46	8.06	133,958
Brazil	*Tayra barbara* **	A4	5.25	5.6	14.03	227.41	17.13	133,952
Brazil	*Tayra barbara* **	A5	10.3	5.5	26.13	243.13	13.42	133,955
Paraguay	*Tayra barbara galina* **	A7	6.02	5.91	16.09	261.88	18.42	36,507
Honduras	*Tayra barbara inserta* **	A8	1.59	0.74	0.53	13.64	5.29	123,271
Honduras	*Tayra barbara inserta* **	A9	2.61	2.46	1.92	44.66	9.09	128,127
Brazil	*Tayra barbara barbara* **	A13	5.08	4.77	10.53	138.99	12.09	37,479
Bolivia	*Eira barbara*	A15	6.4	3.15	5.92	126.57	14.68	38,810
Bolivia	*Tayra barbara madeirensis* **	A16	9.3	5.6	18.25	217.67	14.38	40,838
Trinidad and Tobago	*Tayra barbara trinitatis* **	A17	5.94	5.1	16.19	79.25	5.56	7543–5937
Colombia	*Tayra barbara* **	A18	5.4	5.4	14.57	95.12	7.03	134,947
Colombia	*Tayra barbara barbara* **	A19	10.7	6.18	32.77	303.29	14.95	37,366
Ecuador	*Eira barbara*	A24	9.31	6.99	29.93	226.44	11.68	182,953
Brazil	*Tayra barbara* **	A26	9.9	7.3	30.38	391.45	20.04	133,953
Venezuela	*Tayra barbara barbara* **	A37	8.7	5.1	21.98	273.71	16.47	30,202
Venezuela	*Tayra barbara* **	A38	12.8	5.6	25.91	266.83	14.79	16,937
Venezuela	*Tayra barbara* **	A39	9.9	4.06	20.62	254.03	15.79	16,938
Mexico	*Tayra barbara senex* **	A45	5	3.36	9.05	146.26	13.72	17,254
Colombia	*Tayra barbara* **	A46	1.47	1.07	0.69	32.19	10.93	37,799
Colombia	*Tayra barbara* **	A47	5.25	3.8	7.75	156.42	15.85	37,800
Costa Rica	*Tayra barbara biologiae* **	A48	2.71	1.3	1.3	28.47	7.05	24,444
Ecuador	*Tayra barbara senilis* **	A50	9.5	6.36	28.94	207.24	10.87	36,589
Brazil	TAYRA	A54	2.86	2.42	2.53	84.56	15.00	36,230
Colombia	*Tayra barbara irara* **	A67	8.51	8.14	23.13	206.21	12.10	14,630
Colombia	*Tayra barbara irara* **	A69	8.28	5.03	19.12	207.98	13.42	14,860
Colombia	*Tayra barbara irara* **	A70	4.34	3.91	8.47	104.11	10.09	14,861
Colombia	*Tayra barbara irara* **	A72	4.49	2.8	4.35	74.62	10.10	15,473
Colombia	*Tayra barbara irara* **	A73	6.02	4.65	10.47	165.2	14.41	15,471
Colombia	*Tayra barbara irara* **	A77	1.59	1.74	1.2	39.57	10.19	23,485

Colombia	*Tayra barbara* **	A85	6.96	3.55	12.66	174.13	13.81	14,224
Colombia	*Tayra barbara barbara* **	A87	7.47	8.37	34.32	334.7	16.12	76,747
Colombia	*Tayra barbara barbara* **	A88	8.5	5.28	20.81	201.66	12.47	76,748
Peru	*Eira barbara*	A114	5.27	4.75	11.24	132.79	11.18	230,838
Colombia	*Tayra barbara barbara* **	A138	4.66	1.96	3.67	74.78	11.01	32,669
Colombia	*Eira barbara biologiae* **	S2	6.79	4.36	8.49	78.04	7.56	281,467
Costa Rica	*Tayra barbara biologiae* **	S3	7.38	5.14	17.31	156.75	10.63	8411–38,483
Costa Rica	*Tayra barbara biologiae* **	S4	3.97	2.43	3.11	58.32	9.33	11,375
Costa Rica	*Tayra barbara biologiae* **	S5	7.31	4.44	9.87	169.65	15.24	12,875
Panama	*Tayra barbara biologiae* **	S10	1.18	0.88	0.43	27.94	12.02	171,081
Ecuador	*Eira barbara biologiae* **	S11	4.51	3.17	5.06	101.3	12.71	104,547
Peru	*Eira barbara peruana*	S12	5.82	6.52	12.31	177.98	14.31	149,015
Ecuador	*Taya barbara biologiae* **	S14	8.05	6.2	23.29	199.95	11.69	104,546
Guyana	*Tayra barbara poliocephala* **	S17	11.69	8.38	45.91	307.26	12.80	172,995
Mexico	*Eira barbara senex*	S21	5.78	4.2	11.69	127.81	10.55	181,265
Guatemala	*Eira barbara senex*	S22	2.9	5.9	10.32	97.2	8.54	61,276
Guatemala	*Eira barbara senex*	S23	2.53	2.18	1.88	46.39	9.55	287,480
Mexico	*Eira barbara senex*	S24	6.43	7.25	23.24	117.37	6.87	13,070
Mexico	*Eira barbara senex*	S25	4.59	4.49	8.41	170.18	16.56	100,447
Panama	*Tayra barbara* **	S27	14.7	6.72	49.9	167.15	6.68	15,423
Panama	*Tayra barbara biologiae* **	S38	8.33	3.87	9.08	177.84	16.65	297,961
Panama	*Tayra barbara biologiae* **	S41	4.85	3.36	6.03	92.99	10.69	297,962
Panama	*Eira barbara biologiae* **	S42	3.12	5.99	7.46	167.86	17.34	310,671
Panama	*Eira barbara biologiae* **	S43	2.08	1.4	1.15	29.32	7.71	310,673
Panama	*Eira barbara biologiae* **	S44	2.29	1.94	1.85	42.13	8.74	334,556
Panama	*Eira barbara biologiae* **	S50	0.96	0.69	0.17	16.88	11.55	335,772
Guatemala	*Eira barbara senex*	S68	3.55	1.52	2.32	31.92	5.91	287,482
Venezuela	*Eira barbara poliocephala*	S69	2.07	1.19	0.99	27.95	7.93	296,625
Guatemala	*Eira barbara senex*	S70	3.03	1.76	2.41	31.35	5.70	287,481
Mexico	*Eira barbara*	MX 1	5.68	5.09	12.09	144.87	11.76	CNMA-4160
Mexico	*Eira barbara senex*	MX 2	6.82	5.4	19.48	95.58	6.11	CNMA-188
Mexico	*Eira barbara*	MX 3	8.18	5	19.68	226.21	14.39	ZOOMAT-0311-828
Mexico	*Eira barbara*	MX 4	6.61	6.22	21.23	162.84	9.97	ZOOMAT-726
Mexico	*Eira barbara*	MX 5	6.1	3.59	12.33	86.05	6.91	ZOOMAT-0303-123
Mexico	*Eira barbara senex*	MX 6	8.08	6.24	25.35	141.93	7.95	IIB-UV-3451
Mexico	*Eira barbara*	MX 7	7.24	5.54	18.14	215.82	14.30	ECOSUR-5431
Mexico	*Eira barbara senex*	MX 8	9.24	5.36	20.41	147.81	9.23	ECOSUR-5552
Mexico	*Eira barbara senex*	MX 9	2.61	3.49	4.04	41.7	5.85	ECOSUR-1170

Mexico	*Eira barbara senex*	MX 10	3.54	2.3	2.63	59.35	10.33	ECOSUR-2585
Mexico	*Eira barbara*	MX 11	6.42	5.81	19.09	151.47	9.78	CEDESU–UAC-836
Mexico	*Eira barbara*	MX 12	4.91	3.45	7.51	75.66	7.79	CEDESU–UAC-604
Mexico	*Eira barbara*	MX 13	6.81	5.06	15.59	156.94	11.22	CEDESU–UAC–without number

The letters indicate the name of the Zoological Collection to which the specimen belongs: A = AMNH; S = NMNH–Smithsonian Institution and MX = Zoological Collections of Mexico; CNMA = Colección Nacional de Mamíferos; ZOOMAT = Zoológico Miguel Álvarez del Toro; IBB-UV = Instituto de Investigaciones Biológicas de la Universidad Veracruzana; ECOSUR = El Colegio de la Frontera Sur; CEDESU–UAC = Centro de Estudios en Desarrollo Sustentable y Aprovechamiento de la Vida Silvestre de la Universidad Autónoma de Campeche. * = This is the name given by the original collectors to the specimens; ** = This name is no longer used.

Appendix C

Figura A2-1. *Cont.*

Figure A2: Photographs of the 73 museum specimens of *Eira barbara* examined, showing the differences in shape and size of the throat patches. The letters indicate the name of the Zoological Collection to which the specimen belongs: A = AMNH; S = NMNH–Smithsonian Institution and MX = Zoological Collections of Mexico.

Appendix D

Figure A3-1. Records of *Eira barbara* in the Peruvian Amazon (*Cont.*).

Figure A3-2: Records of *Eira barbara* in the Peruvian Amazon.

The letter corresponds to each identified animal (**b**, **d**, **f** and **i** = males; **a**, **c**, **e**, **g** and **h**, = animals of unknown sex). The records of the same animal correspond to different dates. The circles in the images pointed at the penis and/or testicles of the animal.

Capítulo 2.

Activity patterns of tayra (*Eira barbara*) across their distribution.

El presente capitulo consiste en un esfuerzo internacional entre investigadores de diferentes instituciones, los registros de *Eira barbara* son utilizados con la autorización de los diferentes coautores. Los créditos correspondientes son nombrados a continuación.

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ABSTRACT

Camera trap records provide data to examine habitat use, describe animal behavior, generate estimates of populations and distributions and analyze activity patterns. Assessment of variation in activity patterns can aid to understanding local adaptations of a species. We used camera trap data with the objective to describe and compare the activity patterns of ten populations of tayras (*Eira barbara*) distributed from the south of Mexico to the north of Argentina and to investigate whether activity patterns changed in a consistent manner across this large latitudinal gradient. We used the kernel density estimator based on the time of independent photographic events to calculate the proportion of diurnal, nocturnal and crepuscular activity of tayra. The majority of the activity of the species throughout their range occured during diurnal periods/ daylight phase (79.31%, 759 records), and in a lower proportion in crepuscular periods (18.07%, 173 records). In northern localities, the activity of the species had two different peaks of activity during the day with most of the activity occurred during the morning. In locations closer to the geographical equator, the activity of the species was constant throughout the day, the only peak of activity was reached on midday. In southern localities, the species had both unimodal (the peak of activity was reached around midday) and bimodal (most of the activity occurred during the early hours of the daylight phase or the late afternoon) activity patterns. The overlap coefficient of tayra oscillated between $\Delta_4 = 0.64$ and $\Delta_1 = 0.95$; demonstrating the plasticity of the species to adapt to a wide range of habitats and use a variety of resources. The activity patterns of tayra varied slightly between seasons. Knowledge of the activity patterns is necessary to desiging management and recovery actions for threatened species.

Keywords: Carnivores, Mustelidae, Neotropics, Noninvasive survey, Overlap analyses.

INTRODUCTION

Activity patterns are an important component of the natural history of an organism and provide insight into the role and the ecology of a species within their ecosystem (González-Maya *et al*., 2009). Activity patterns vary in relation to a variety of biotic and abiotic factors such as length of day, temperature (Kronfeld-Schor & Dayan 2003; Roll *et al*. 2006), prey availability (Clark, 1951; McDonough & Loughry 1997; Halle & Stenseth, 2000), luminosity (Aliaga-Rossel 2004), and rainfall (Smythe, 1978). The activity patterns of a species reflect the need to meet their basic requirements of food, social interactions, movement and rest (Beier & McCullough, 1990). These patterns may vary depending on the intrinsic characteristics of an individual (e.g.sex, age, physiological state, and external factors such as the quality of the habitat (Marchinton & Hirth, 1984; Beier & McCullough, 1990; López-Tello *et al*., 2015). In addition, it is clear that human activities can cause changes in the activity patterns of wild species, such as those that are hunted (Di Bitetti *et al*., 2008; Espinosa & Salvador, 2017).

Eira barbara (hereafter, tayra) is a Neotropical mustelid distributed from the coasts of central Mexico to northern Argentina (Presley, 2000). Previous studies indicate that the species has diurnal habits, with peaks of activity in the early morning and late afternoon, with occasional nocturnal activity occuring until midnight (Kaufmann & Kaufmann, 1965; Defler, 1980; Konecny, 1989; Sunquist *et al*., 1989; Presley, 2000). Dispersal across open areas (Defler, 1980) and some sexual activity (Kaufmann and Kaufmann, 1965) have been reported at night (Presley, 2000). In zones with anthropogenic disturbance the activity of the species is predominantly crepuscular (Emmons & Feer, 1997). Very few studies in general have focused exclusively on tayra, and for this reason basic aspects of their ecology remain unknown.

Through the analysis of camera trap data, the activity patterns of the species has been described in some populations of South America. Delgado *et al*. (2011) demonstrated that the species had diurnal activity, with more pronounced activity peaks occurring at noon and during sunset. Their records were obtained in a small ecological reserve integrated by disturbed primary forest in Colombia. González-Maya *et al*. (2015) found that tayra were primarily diurnal in two populations from Costa Rica and Colombia although the level of overlap between the activity patterns in the two countries was only 68.5%. Albanesi *et al.* (2016) reported that in different areas in the Yungas of Argentina tayras were diurnal during the dry season (74% of records), with appreciable crepuscular activity and were slightly inactive during midday. During the rainy season in these populations, the tayra had greater diurnal activity (82.2%), and less crepuscular activity.

The objective of the present study was to describe and compare the activity patterns of different populations of tayras distributed throughout the Neotropics. Within this general objective, we analyzed whether activity patterns variation, if present, was associated with changes in latitudinal gradient and also compared the activity patterns of a single site between the rainy and the dry season. We postulated that the activity of the species depended on the length of the daylight phase coupled with the abiotic characteristics of the environment. We hypothesized that diel activity patters of tayra will be different between populations along or close to the geographical equator when compared with those at higher or lower latitudes. Because daily conditions can change significantly between seasons, we also hypothesized that diel activity patterns of tayra will differ between different seasons in a single site.

METHODS

Study area

The photographic records of tayras were obtained in 10 study areas throughout the species' range from Mexico to Argentina (Figure 2-1). These areas encompassed a wide variety of biotic and abiotic conditions (Table 2-1). Study area varied in elevation (0 to 3.090 meters above sea level), climatic seasonality (areas with a distinct dry and rainy season to areas without a distinct dry season) average annual precipitation (1,000 to 4,300 mm) and average annual temperature (12.9 to 36.9 ° C).

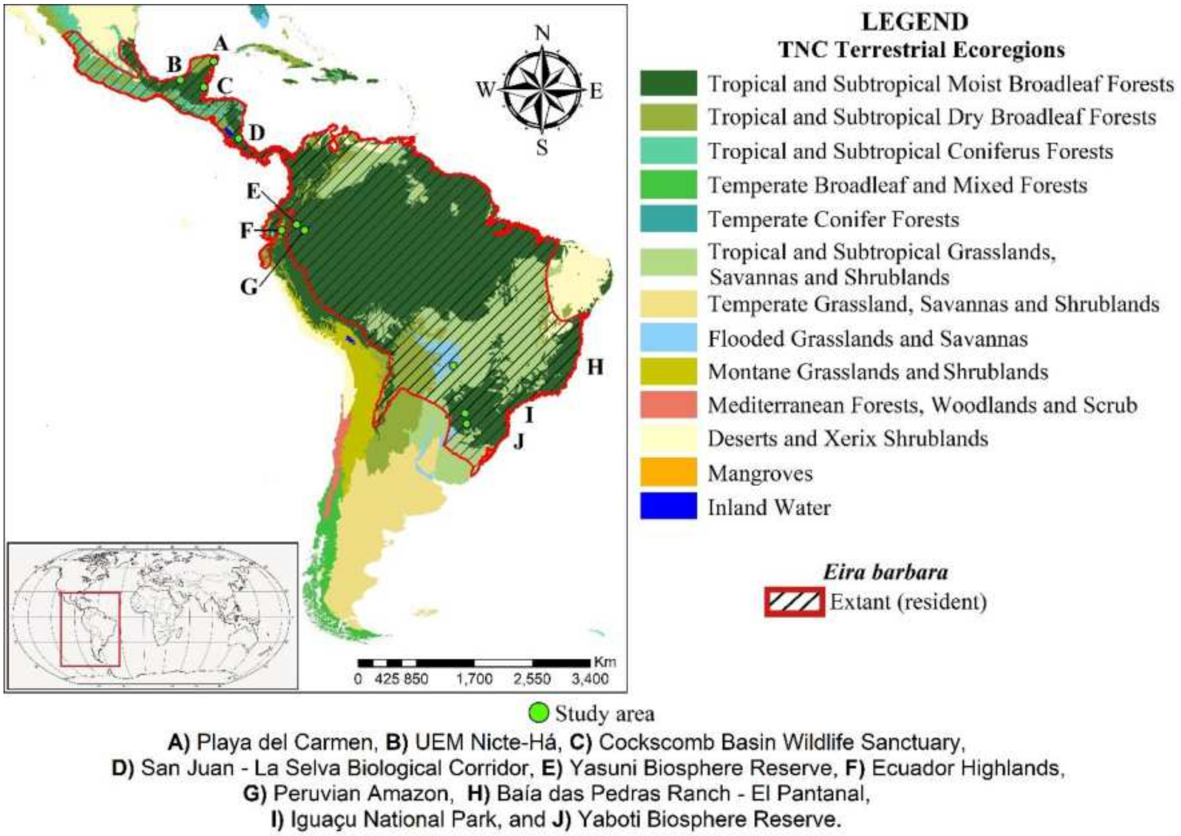

Fig. 2-1. Study localities (n = 10) where we detected the presence of *Eira barbara* (map modified from Olson *et al*., 2001; International Union for Conservation of Nature, 2016).

Camera-trap data

The photographic records of tayra analyzed in this research were the product of projects with various objectives focused on the study of different species. For this reason, the extent of the study area, the period of monitoring, sampling effort, and the characteristics and distribution of camera trap stations all varied significantly. However, all cameras were active 24 hours per day and used either infrared or white flash at night. We identified the date and hour from each tayra record. At the same camera station, only those photographs by 24 h cycles were considered as independent events.

Table 2-1. Description of the study areas, including their camera survey characteristics, used to describe tayra activity patterns across their geographic range.

Country	Locality	Elevation (m asl*)	Habitat types	Terrestrial Ecoregion[1]	Weather [2]	Average annual precipitation (mm)	Average annual temperature (° C)	Climatic seasonality	Sampling period	Sampling effort (Camera – days)	Independent records of Tayra	Relative abundance (# records / sampling effort * 100)
Mexico	Playa del Carmen	0 – 10	A gradient of successional stages that include induced pastures and seasonal agriculture, second growth forests, and mature tropical forests [M1]	Tropical and Subtropical Moist Broadleaf Forests	A*w* (Equatorial savannah with dry winter)	1,552	26° - 28°	Dry (Jan - Jun), Rainy (July - Nov), [M1]	Jan – Jun, and July - Nov	8,838	81	0.91
	Unit Environnemental Management Nicte-Há	0 - 3	Swamps vegetation, dry deciduous forest, and tropical deciduous forest [M2]			1,100 - 2,000	> 26°	Dry (Feb - May), Rainy (Jun-Sep), Nortes (Oct-Mar) [M2]	Feb - June	10,335	74	0.71
Belize	Cockscomb Basin Wildlife Sanctuary	50 - 1,120	A mixture of evergreen and semi-evergreen broadleaf tropical forest and a mosaic of regenerating secondary forest in several stages of succession [BE]		A*m* (Equatorial moonson)	2,700	25° - 28°	Dry (Jan - May), Rainy (Jun - Dec)	Jan - Dec	38,083	189	0.49
Costa Rica	The San Juan–La Selva Biological Corridor	35 - 137	Lowland tropical rainforest and agricultural plantations [CR]		A*f* (Equatorial rainforest, fully humid)	4,300	25°	Dry (Nov April), Rainy (May - Nov)	June - Aug	2,921	33	1.12
Ecuador	Yasuni Biosphere Reserve	204 - 365	Evergreen tropical terra firme forest [EC1]		A*f* (Equatorial rainforest, fully humid)	3,000	22° - 34°	There is no distinct dry season	Jul - Mar	9,506	52	0.54

	Ecuador Highlands	1,520 - 3,090	Lower montane rain forest and high altitude cloud forest [EC2]	Tropical and Subtropical Dry Broadleaf Forest	C*fb* (Warm temperate climate, fully humid)	1,670	12.9 º	There is no distinct dry season; the rainfall increases from Jan/Mar to Sep/Oct	Jul - Mar	8,768	35	0.39
Peru	Peruvian Amazon near the Ecuador border	205 -279	Lowland tropical rainforest [PR1]	Tropical and Subtropical Moist Broadleaf Forests	A*f* (Equatorial rainforest, fully humid)	2,500 - 3,000	36.9° [PR2]	There is no distinct dry season	April - Sep	3,068	35	1.14
Brazil	Baía das Pedras Ranch, El Pantanal	0	Seasonal floodplains, open grasslands, semi-deciduous forest, cerrado forest [BR1]	Flooded Grasslands and Shrublands	*Aw* (Equatorial savannah with dry winter)	1,000 - 1,300	21.5º	Dry (Apr – Sep), Rainy (Oct – March)	Jan - Dec	9,999**	337	3.37
	Iguaçu National Park	200 - 700	Semi-deciduous forest and araucaria forest [BR2]	Tropical and Subtropical Moist Broadleaf Forests	*Cfa* (Warm temperate, fully humid)	1,712	20.7º	There is no distinct dry season [BR2, AR]	Jul - May	12,280	76	0.61
Argentina	Yaboti Biosphere Reserve	200 - 500	Subtropical Moist Broadleaf Forests [AR]			2,169	19.6°		Mar - Dec	2,427	45	1.85

* = meters above sea level. 1= Olson *et al*., 2001; 2= Kottek *et al*., 2006; AR= Di Bitetti *et al*., 2008; BE= Kamstra, 1987; BR1= Mangini *et al.,* 2012; BR2= da Silva *et al*., 2018; CR= Cove *et al*., 2014; EC1= Espinosa, 2012; EC2= Reyes-Puig *et al*., 2015; Ríos-Alvear, 2016; M1= Hidalgo-Mihart *et al*., 2017; M2= Guerra-Santos & Kahl, 2018; PR1= Kolowski & Alonso, 2010; and PR2= Fick & Hijmans, 2017. **= data not confirmed by the author.

Activity patterns

We extracted the date and time, as well as geographic coordinates, of each independent photographic capture of tayra. To compare the data from different study areas, we transformed every date to Julian days with the program provided by the United States Naval Observatory (USNO, 2018) and converted the photographic record time of each photograph to solar time with R-package *solaR* (Perpiñán, 2012). We used the Kernel density estimator (Ridout & Linkie, 2009) to generate the activity patterns in each study area. We used all the records of tayra to generate a general activity pattern of the species throughout their distribution. Because time of sunrise and sunset varies with latitude, we calculated the average time between sunrise and sunset for each study area with the R-package Ratmosphere (Biavati, 2015) to allow comparison of different study areas.

We categorized activity as: (1) diurnal, one hour after sunrise to one hour before sunset; (2) nocturnal, one hour after sunset to one hour before sunrise; and (3) crepuscular, one hour before and after sunrise, and one hour before and after sunset (Foster *et al*., 2013).

To compare the activity patterns of tayra between different study areas, for each possible pair of sites, we calculated the overlap coefficient (Δ) and estimated 95% confidence interval with *bootstrap* using 10,000 samples (Meredith & Ridout, 2017). The overlap coefficients used were based in the number of records of each study area. We used Δ_1 in the localities where we obtained less than 50 records of tayra (Costa Rica, Ecuador Highlands, Peruvian Amazon, and Yaboti Biosphere Reserve), and Δ_4 for the localities with more than 50 records of the species (Playa del Carmen, UEM Nicte-Há, Cockscomb, Yasuni Biosphere Reserve, Baía das Pedras Ranch, and Iguaçu National Park). Overlap values range from 0 (no overlap) to 1 (total overlap). This analysis was performed with the R-package *overlap* (Meredith & Ridout, 2017).

To compare the diurnal activity of tayra across its distribution, non-parametric correlation was used to test the relationship between the percentage of activity of the species during the daylight phase and the latitudinal location of each study area. With the objective to compare the daylight activity of the species across the distribution of the study areas, we made a correlation between the percentage of diurnal activity of the species and the latitudinal distance of each study area to the geographical equator.

In study areas with notable climatic seasonality (Playa del Carmen, UEM Nicte-Há, Cockscomb, and Baía das Pedras Ranch), we used the Kernel density estimator (Ridout & Linkie, 2009) to generate the activity patterns of tayra during both the dry season and the rainy season. We calculated the overlap coefficient in the same study area during these different climatic seasons; we used Δ_1 for the records from Playa del Carmen and UEM Nicte-Há, we used Δ_4 for the records from Cockscomb and Baía das Pedras Ranch. Records from Costa Rica were not compared here because these data were only obtained during the rainy season.

RESULTS

We obtained 957 independent records of tayras at 10 locations in the Neotropics. The pooled results indicated that the majority of the activity of the species occurred during the diurnal period (79.31%, 759 records, Fig. 2-2). We also observed two peaks of activity, the first occurred during the early hours of the morning (9:00 to 10:59 hrs), activity began to decline from 11:00 hrs, reached the lowest diurnal point at 13:00 hrs, and a second, lower activity peak ocurred around 15:00 hrs. The activity of tayra also ocurred during crepuscular periods (18.07%, 173 records). Activity increases rapidly at sunrise and with a more gradual decrease at sunset. Only 2.61% (25 records) of all tayra activity records occurred during the nocturnal period. The maximun proportion of nocturnal records for a study areas was 6.67% and four study areas did not record nocturnal activity (Table 2-2).

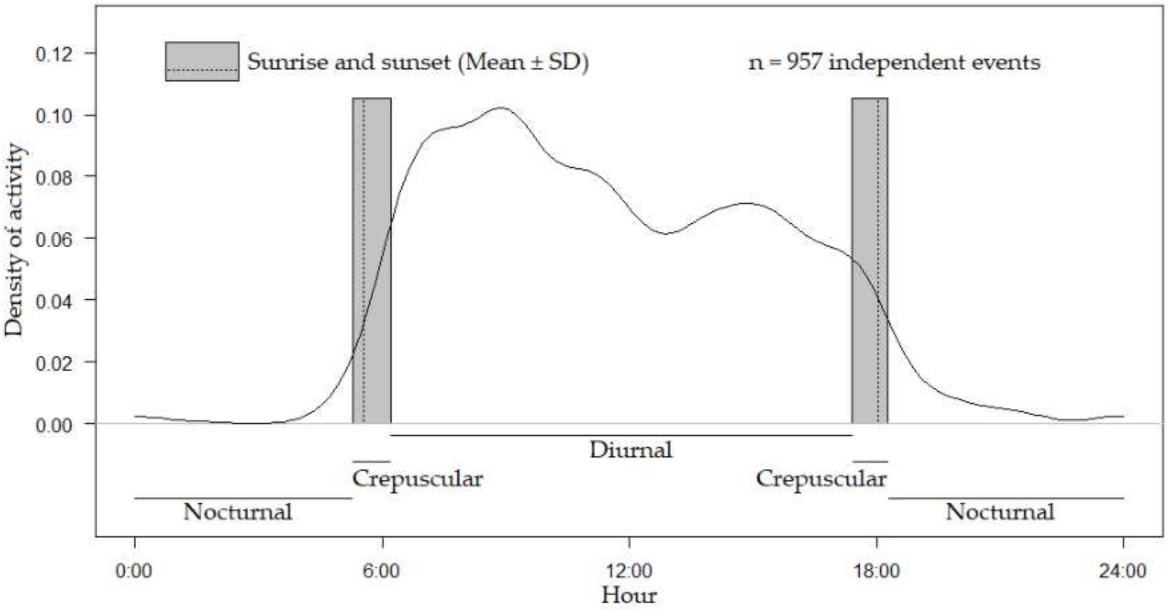

Fig. 2-2. General activity pattern of *Eira barbara* throughout its distribution, estimated through a density function that measures the probability of observing the animal during categorized periods throughout the day.

Table 2-2. *Eira barbara* activity patterns in 10 study areas throughout its distribution.

Country	Study area	Latitudinal location*	Categories of the day			
			Diurnal	Nocturnal	Crepuscular	
					Sunrise	Sunset
Mexico	Playa del Carmen (n = 81)	20.76	76.54%	2.47%	12.35%	8.64%
	UEM Nicte-Há (n = 74)	18.22	81.08%	4.05%	6.76%	8.11%
Belize	Cockscomb Basin Wildlife Sanctuary (n = 189)	17.02	85.19%	2.12%	6.35%	6.35%
Costa Rica	San Juan - La Selva Biological Corridor (n = 33)	10.50	84.85%	0	9.09%	6.06%
Ecuador	Yasuni Biosphere Reserve (n = 52)	-0.88	96.15%	0	0	3.85%
	Ecuador Highlands (n = 35)	-0.95	94.29%	0	0	5.71%
Peru	Peruvian Amazon (n = 35)	-1.80	94.29%	0	0	5.71%
Brazil	Baía das Pedras Ranch (n= 337)	-19.30	70.33%	3.86%	18.69%	7.12%
	Iguaçu National Park (n = 76)	-25.53	84.21%	1.32%	3.95%	10.53%
Argentina	Yaboti Biosphere Reserve (n = 45)	-26.91	75.56%	6.67%	4.44%	13.33%
	Total Continental (n = 957)		79.31%	2.61%	10.34%	7.73%

* = decimal degrees.

While activity of tayra in the 10 localities occurred mainly during the diurnal period, we observed variation in the timing of the peaks of diurnal activity. In the study areas located in the northern hemisphere, the highest peak of activity was observed during the first hours of the daylight phase, and slightly decreased around midday (11:00 – 13:00 hrs), with a second peak of activity during the afternoon (Fig. 2-3B, C and D). In Playa del Carmen, a single peak of activity occurred during the first hours of the daylight (Fig. 2-3A), and activity remained at a constant lower level during the rest of the day and completely ceased by the first hour of the night.

In study areas located in the southern hemisphere near the geographical equator, the activity of tayra began during the first hours of the daylight phase, with a single peak of activity around noon (11:00 – 13:00 hrs; Fig. 2-3E-G). In the study areas located in the southern hemisphere at more northern latitudes, the activity of the species did not show any specific trend. In Baía das Pedras Ranch, the highest peak of activity occurred during the first hours of the daylight (Fig. 2-3H), and slightly decreased around midday (12:00 – 13:00 hrs), the activity slightly increased and remain with fluctuations during the afternoon. The activity of tayra started to decrease in the sunset and remain active until midnight.

In Iguaçu National Park the activity of tayra began during the first hours of the daylight phase, with a single peak of activity around noon (11:00 – 13:00 hrs; Fig. 2-3I). The activity of the species began to decrease progressively from midday and ceased completely the first hours of the night (two hours after the sunset).

In Yaboti Biosphere Reserve, the activity of the species began during the morning and slightly decreased around midday (11:00 – 13:00 hrs), with the highest peak of activity occuring during the afternoon (Fig. 2-3J). The species remained slightly active until midnight.

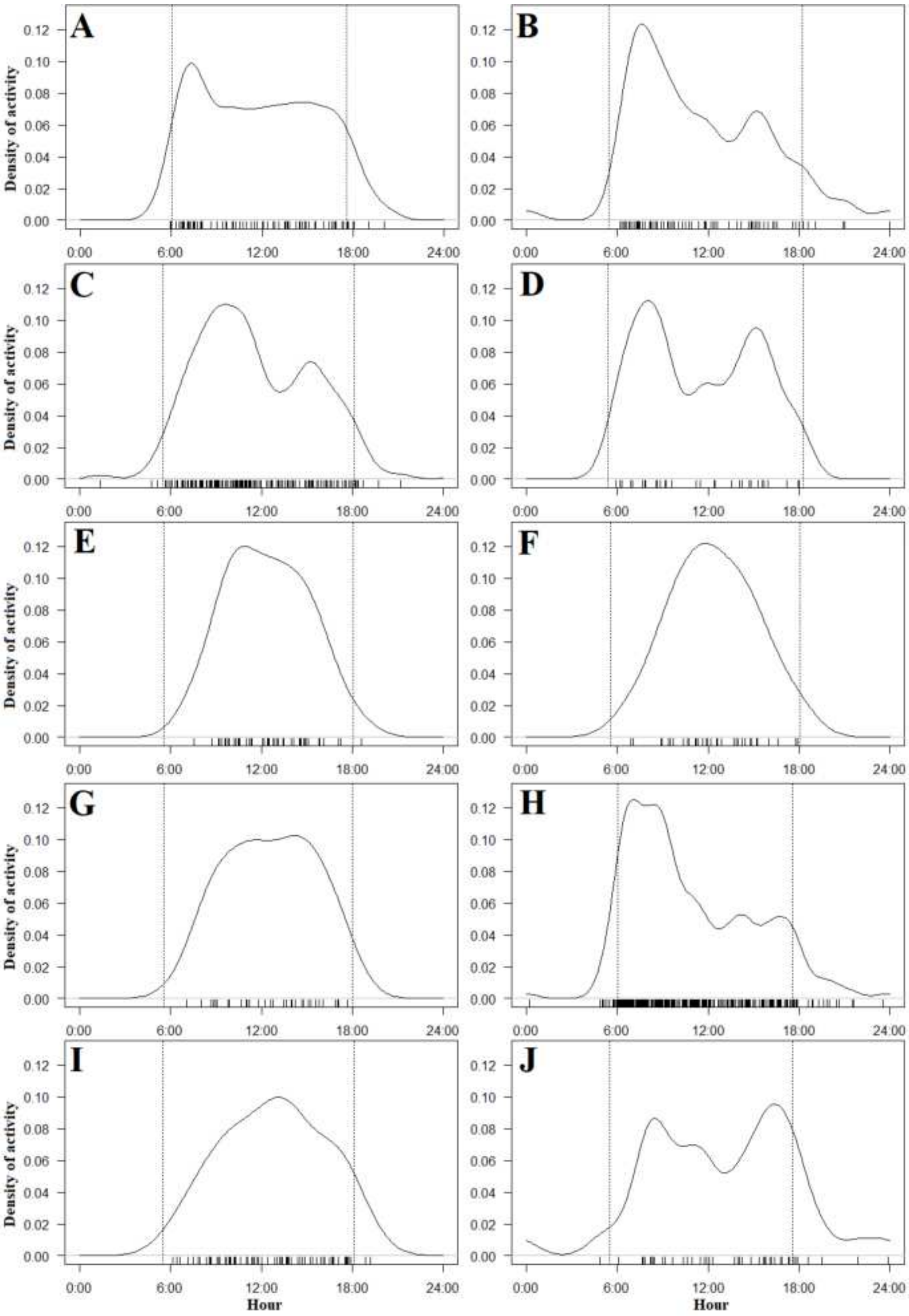

Fig. 2-3. Activity pattern of *Eira barbara* in different study areas: A) Playa del Carmen (Mexico), B) UEM Nicte-Há (Mexico), C) Cockscomb Basin Wildlife Sanctuary (Belize), D) San Juan - La Selva Biological Corridor (Costa Rica), E) Yasuni Biosphere Reserve (Ecuador), F) Ecuador Highlands (Ecuador), G) Peruvian Amazon (Peru), H) Baía das Pedras Ranch (Brazil), I) Iguaçu National Park (Brazil), and J) Yaboti Biosphere Reserve (Argentina). The vertical dashed lines represent the mean time of sunrise and sunset.

The overlap coefficients of activity patterns of tayra varied among study areas (from $\Delta_4 = 0.69$ to $\Delta_1 = 0.95$, Table 2-3). We found a significant quadratic adjustment (r^2 quadratic= 0.58, r= 0.15) between the percentage of diurnal activity of the species during the daylight phase and the latitudinal location of each study area (Fig. 2-4).

Table 2-3. Overlap values of the activity patterns of *Eira barbara*, and latitudinal distance (decimal degrees*) between the study areas.

Country	Mexico		Belize	Costa Rica	Ecuador		Peru	Brazil		Argentina
Study area	Playa del Carmen	UEM Nicte-Há	Cockscomb Basin Wildlife Sanctuary	San Juan - La Selva Biological Corridor	Yasuni Biosphere Reserve	Ecuador Highlands	Peruvian Amazon	Baía das Pedras Ranch, El Pantanal	Iguaçu National Park	Yaboti Biosphere Reserve
Playa del Carmen	-	$\Delta_4 = 0.88$	$\Delta_4 = 0.87$	$\Delta_1 = 0.90$	$\Delta_4 = 0.74$	$\Delta_1 = 0.76$	$\Delta_1 = 0.80$	$\Delta_4 = 0.83$	$\Delta_4 = 0.85$	$\Delta_1 = 0.84$
UEM Nicte-Há	2.54	-	$\Delta_4 = 0.86$	$\Delta_1 = 0.88$	$\Delta_4 = 0.69$	$\Delta_1 = 0.71$	$\Delta_1 = 0.73$	$\Delta_4 = 0.91$	$\Delta_4 = 0.74$	$\Delta_1 = 0.82$
Cockscomb Basin Wildlife Sanctuary	3.74	1.20	-	$\Delta_1 = 0.85$	$\Delta_4 = 0.80$	$\Delta_1 = 0.80$	$\Delta_1 = 0.82$	$\Delta_4 = 0.82$	$\Delta_4 = 0.82$	$\Delta_1 = 0.83$
San Juan - La Selva Biological Corridor	10.28	7.73	6.53	-	$\Delta_1 = 0.72$	$\Delta_1 = 0.73$	$\Delta_1 = 0.78$	$\Delta_1 = 0.85$	$\Delta_1 = 0.77$	$\Delta_1 = 0.80$
Yasuni Biosphere Reserve	21.64	19.10	17.90	11.36	-	$\Delta_1 = 0.95$	$\Delta_1 = 0.91$	$\Delta_4 = 0.64$	$\Delta_4 = 0.86$	$\Delta_1 = 0.71$
Ecuador Highlands	21.71	19.17	17.97	11.43	0.07	-	$\Delta_1 = 0.91$	$\Delta_1 = 0.66$	$\Delta_1 = 0.87$	$\Delta_1 = 0.72$
Peruvian Amazon	22.56	20.02	18.82	12.28	0.91	0.84	-	$\Delta_1 = 0.68$	$\Delta_1 = 0.91$	$\Delta_1 = 0.78$
Baía das Pedras Ranch, El Pantanal	40.06	37.52	36.32	29.78	18.42	18.35	17.50	-	$\Delta_4 = 0.70$	$\Delta_1 = 0.76$
Iguaçu National Park	46.30	43.76	42.55	36.02	24.65	24.58	23.73	6.23	-	$\Delta_1 = 0.84$
Yaboti Biosphere Reserve	47.68	45.13	43.93	37.40	26.03	25.96	25.11	7.61	1.37	-

* = distance in decimal degrees between the latitudinal location of two different sites.

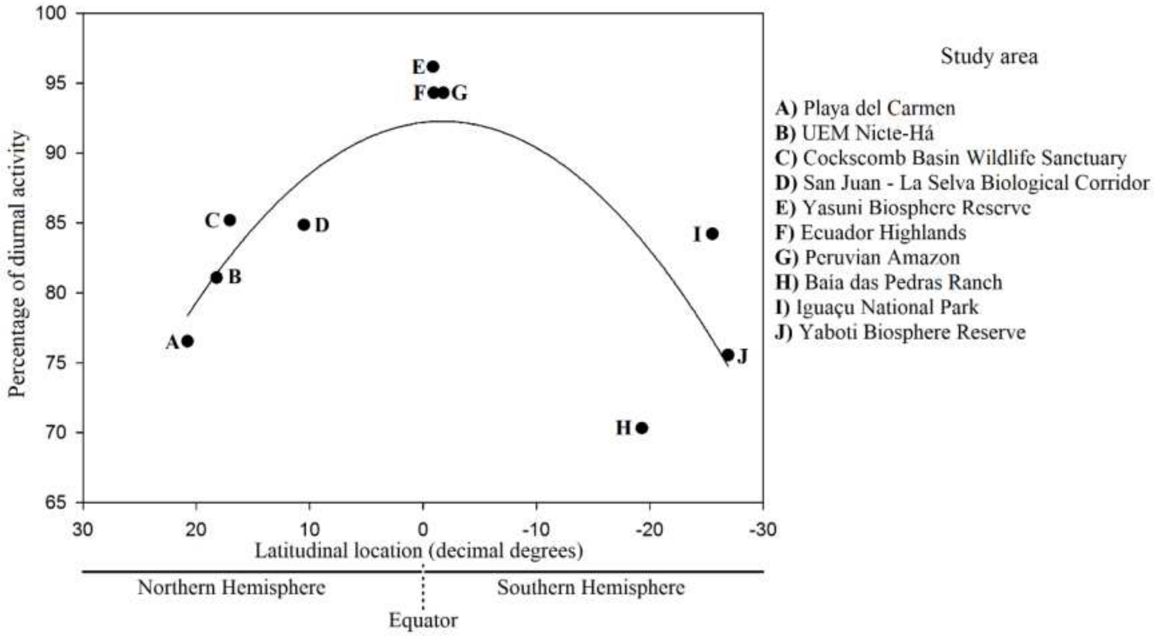

Fig. 2-4. Nonparametric correlation between the latitudinal location and the percentage of diurnal activity of *Eira barbara* in each study area.

We found a significant negative correlation (r^2=0.70, p = -0.84) between the percentage of diurnal activity of the species and the latitudinal distance of each study area to the geographical equator (Fig. 2-5).

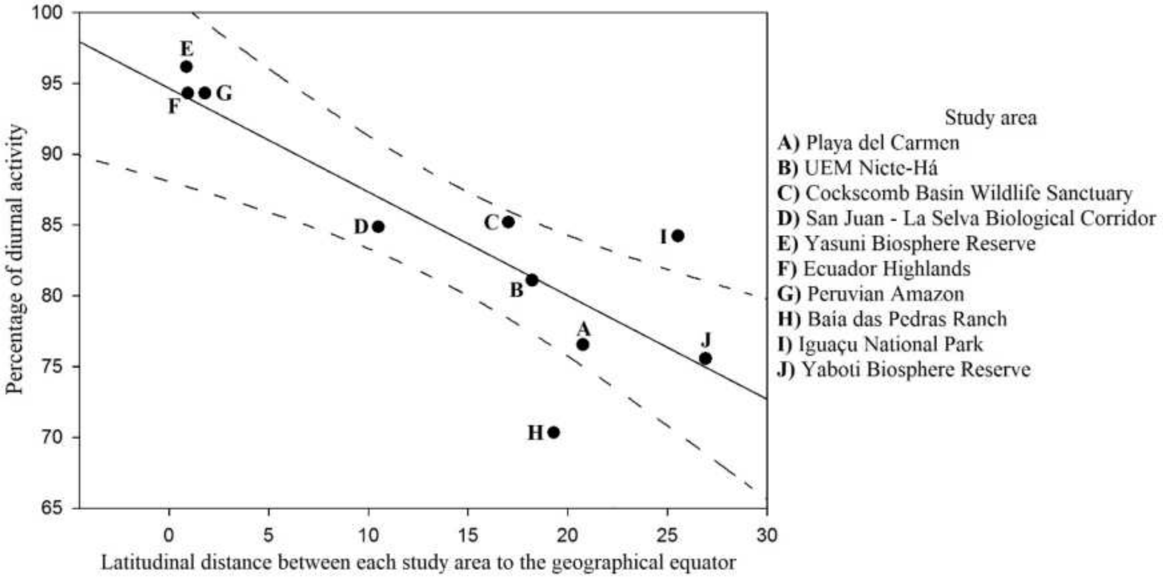

Fig. 2-5. Negative correlation between the latitudinal distance of every study area to the geographical equator and the percentage of diurnal activity of *Eira barbara* in each study area. $y = 94.63 – 0.73 * x$.

In the localities with climatic seasonality, we observed slight differences in the activity of tayra between the dry season and the rainy season (Table 2-4, Fig. 2-6).

Table 2-4. Activity patterns of *Eira barbara* in localities with climatic seasonality.

Country	Study areas	Categories of the day			
		Diurnal	Nocturnal	Crepuscular	
				Sunrise	Sunset
Mexico	Playa del Carmen				
	Dry season (n = 49)	69.38%	2.04%	16.32%	12.24%
	Rainy season (n = 32)	81.25%	0	9.37%	9.37%
	UEM Nicte-Há				
	Dry season (n = 40)	80.00%	7.50%	7.50%	5.00%
	Rainy season (n = 34)	85.29%	0	5.88%	8.82%
Belize	Cockscomb Basin Wildlife Sanctuary				
	Dry season (n = 109)	84.40%	1.83%	7.33%	6.42%
	Rainy season (n = 80)	83.75%	2.50%	7.50%	6.25%
Brazil	Baía das Pedras Ranch, El Pantanal				
	Dry season (n = 236)	69.91%	5.50%	17.79%	6.77%
	Rainy season (n = 101)	73.26%	0.99%	16.83%	8.91%

In Playa del Carmen (Mexico), the diurnal activity of tayra was higher during the rainy season (81.25%) compared with the dry season (69.38%). The species was more active in the early morning and around midday during the rainy season. During the dry season tayra was active in the morning and afternoon with a slight decrease of activity around midday. We obtained only one nocturnal record of the species during the rainy season. The crepuscular activity of tayra was higher in the rainy season (28.56%) than in the dry season (18.74%). The overlap coefficient of the activity patterns of tayra between the dry and the rainy season was $\Delta_1 = 0.80$ (Fig. 2-6A).

In the UEM Nicte-Há (Mexico) the diurnal activity of tayra was only slightly higher during the rainy season (85.29%) compared with the dry season (80.00%). The species was more active in the morning during the dry season, in the rainy season tayra was active in the morning and afternoon with a slightly decrease of activity around midday. Tayra were active in the nocturnal period of the day (three records) only in the dry season. We did not obtain nocturnal records of the species during the rainy season. The crepuscular activity of tayra was higher in the rainy season (14.70%) than in the dry season (12.50%). The overlap coefficient of the activity patterns of tayra between the dry and the rainy season was $\Delta_1 = 0.77$ (Fig. 2-6B).

In Cockscomb Basin Wildlife Sanctuary (Belize) the diurnal activity of tayra was nearly the same during the dry season (84.40%) when compared with the rainy season (83.75%). The species was more active in the morning and afternoon during the dry season (with a slight decrease of activity around midday), in the rainy season tayra was more active in the morning. The nocturnal activity of the species was also very similar in the rainy season (2.50%) than in the dry season (1.83%). The crepuscular activity percentage was the same in both seasons (13.75%), in the dry season we obtained 15 independent records of tayra, in the rainy season we obtained 11 records of the species. The overlap coefficient of the activity patterns of tayra between the dry and the rainy season was $\Delta_4 = 0.90$ (Fig. 2-6C).

In Baía das Pedras Ranch, (Brazil) the diurnal activity of tayra was higher during the rainy season (73.26%) compared with the dry season (69.91%). The species was more active in the early hours of the morning than in the afternoon during both the dry season, and the rainy season with the activity peak shifting slightly later in the morning during the rainy season. The nocturnal activity of the species was higher in the dry season (5.50%) than in the rainy season (0.99%). The crepuscular activity of tayra was higher in the rainy season (25.74%) than in the dry season (24.56%). The overlap coefficient of the activity patterns of tayra between the dry and the rainy season was $\Delta_4 = 0.84$ (Fig. 2-6D).

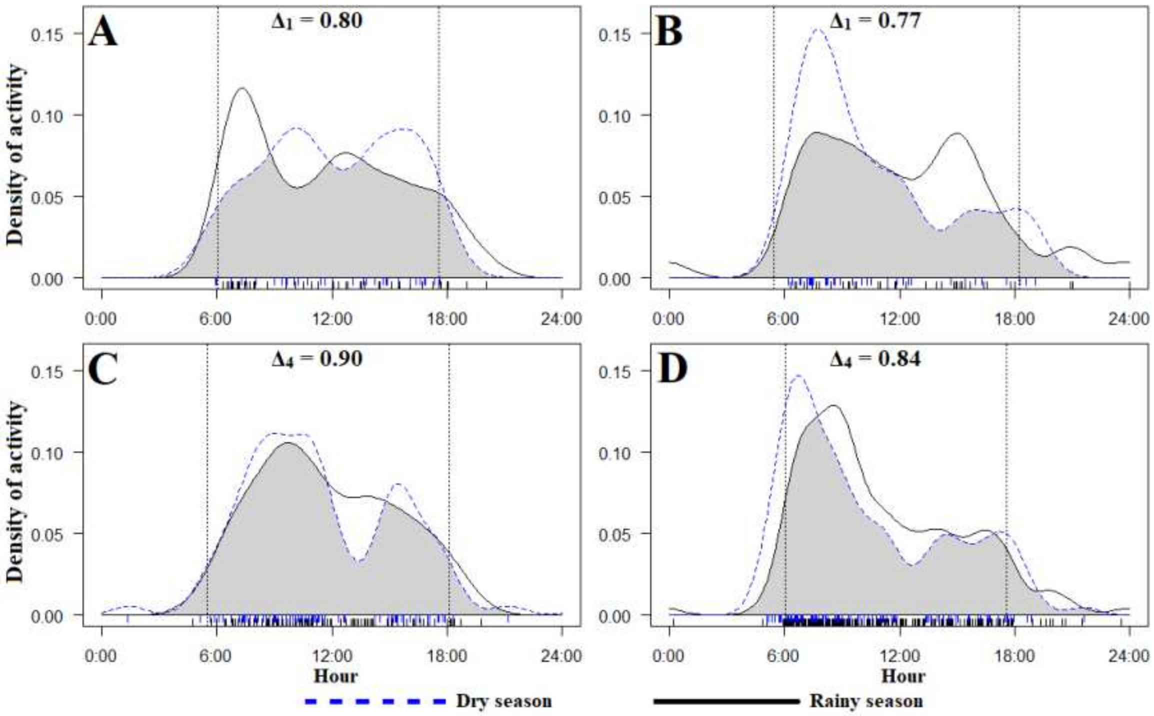

Fig. 2-6. Activity pattern of *Eira barbara* in study areas with climatic seasonality. The vertical dashed lines represent the mean time of sunrise and sunset. A = Playa del Carmen (Mexico), B = UEM Nicte-Há (Mexico), C = Cockscomb Basin Wildlife Sanctuary (Belize), D = Baía das Pedras Ranch (Brazil).

DISCUSSION

Our results demonstrate that the tayra exhibits diurnal habits throughout its distribution. Despite variation in abiotic and biotic factors (altitude, temperature, prey availability, day length, and precipitation) across study sites, the majority of activity (overall = 79.31%, range = 06:55 to 17:04 hrs) occurred during the daylight phase, with a lower proportion during crepuscular periods (18.07%, range = 05:02 to 06:52 hrs in the sunrise and from 17:04 to 19:00 hrs during the sunset). The estimated overlap coefficient ranges between $\Delta_4 = 0.64$ and $\Delta_1 = 0.95$ throughout the study areas, which suggests that tayra activity patterns are fairly plastic in a wide range of habitats and even to close proximity to human settlements (Presley, 2000). In our results, we did not observe an increase of nocturnal activity of the species in study areas closer to human settlements.

The fundamental ecological niche of a species is made up of the set of conditions and resources in which an organism can survive and reproduce (Elton, 2001). Abiotic factors (temperature, time of day, light, environmental precipitation, relative humidity, wind speed) and biotic (availability of prey, presence of predators, intraspecific or interspecific competition) that regulate the activity of a species change during the year and in the course of the day (Halle & Stenseth, 2000). Since periods of activity are energetically expensive, they represent an increased risk of predation and thermal stress. Several mammals use strategies to optimize the amount of time that it is active and reduce risks (Dirzo *et al.*, 2011).

Previous research have reported that the temperature and daylight phase length actively influence the activity patterns of mammals (Kronfeld-Schor & Dayan 2003; Roll *et al.*, 2006; Norris *et al.*, 2010). For mammals, the upper thermal limits oscillate from 10° to 40° C (Bennett *et al.*, 2018). In five study areas (UEM Nicte-Há, Cockscomb, San Juan – La Selva Biological Corridor, Baía das Pedras Ranch, and Yaboti Biosphere Reserve) the activity of tayra decreased around midday, potentially due to the higher daytime temperatures at these sites. Diurnal small mammals in order to reduce the exposure to physiologically stressful conditions generally tend to avoid extreme environmental conditions (Vispo & Bakken, 1993; Bozinovic *et al.*, 2000; Vieira *et al.*, 2010), including the reduction of midday activity (Kronfeld-Schor *et al.*, 2001).

The decrease in the activity of tayra near midday at these locations may serve to avoid thermal stress and thus to limit the energy cost of the search for resources. The low activity or lack of activity during nocturnal periods may be an adaptation to reduce the risk of predation. In most of our study areas (except Biological Corridor, Yasuni Biosphere Reserve, Ecuador Highlands and Peruvian Amazon), tayra were recorded during the nocturnal period, and probably the species is active during the night (2.61 %) to avoid high temperatures of the day, although this may increase the risk of depredation. Some researchers have reported that body size is the main factor influencing mammals activity patterns. Small sized mammals (< 1 kg) are nocturnal as an anti-predation strategy, whereas some larger mammals (> 10 kg) have cathemeral habits (species with discrete periods of activity during both the day and night; LaFleur *et al*., 2014) because of energy requirements and associated feeding commitments (Van Schaik & Griffiths, 1996; Gomez *et al*., 2005).

The crepuscular activity of tayra probably depends on the amount of time that the species was active during the diurnal period. If the species is more active during the daylight phase, its activity during the crepuscular period is lower; however when the species is less active during the day, it has to increase their crepuscular activity as a mechanism to compensate for their lack of activity. Thermal constraints may limit nocturnal activity when nighttime temperatures are low, and diurnal activity when temperatures are high (Bennie *et al*., 2014).

Activity patterns of predators can vary due to the availability of prey (McDonough & Loughry 1997). The activity pattern of prey represents a temporal pattern of food availability (Halle & Stenseth, 2000). Currently, we know little about the trophic niche of tayra, wich as been diferentially classified as an opportunistic omnivore (Presley, 2000), insectivore-omnivore (da Silva & Mendes, 2008), or a frugivore that also feeds on other vertebrates (Mcnab, 1995). The activity of tayra in different study areas could therefore be largely related to foraging and travel time to search for prey or resources. Another factor that can regulate activity patterns of this species could be related to the presence or absence of predators. Information on the predators of tayra is scarce, however, tayra remains have been identified in ocelot scats (Bianchi *et al*., 2010). In some locations of the Brazilian Atlantic Forest Reseves the overlap activity patterns between ocelots and tayras is $\Delta_4 = 0.38$ (Massara *et al*., 2016). Likely tayra is also preyed by larger cats such as puma and jaguar which feed on other smaller carnivores (e.g., Taber *et al*., 1997; Garla & Setz, 2001; Oliveira & Pereira, 2014).

In South America 40 species of terrestrial mammalian carnivores occur, these species share many attributes that may predispose them to competitive interactions (Hunter & Caro; 2008). Several of these species are known to coexist throughout vast geographic areas, showing considerable overlap in range and habitat usage (e.g., *Panthera onca*, *Puma concolor*, *Speothos venaticus*, *Eira barbara*, and *Nasua nasua*; Oliveira & Pereira; 2014; *Leopardus pardalis*; Massara *et al*., 2016). Despite clear differences in temporal activity patterns some middle sized species (such as *Nasua nasua*, *Eira barbara*, and *Herpailurus yagouaroundi*) are potentially under threat from predation by ocelots (Oliveira & Pereira, 2014; Massara *et al*., 2016). Probably the temporal activity partitioning is the mechanism that' allows the coexistence of ocelots and other mesocarnivores (Massara *et al*., 2016), the interactions between species may vary across habitat or land-use gradients (Lewis *et al*., 2015).

Our results in the localities near to the geographical equator (Yasuni Biosphere Reserve, Ecuador Highlands and Peruvian Amazon) indicate that the activity of the species is unimodal. The activity generally increases progressively during the day, reaches a single peak of activity around noon, and decreases progressively during the afternoon. These results are different to those detailed in the literature that reports that tayra has peaks of activity in the early morning and late afternoon (Kaufmann & Kaufmann, 1965; Defler, 1980; Konecny, 1989; Sunquist *et al*., 1989). A possible explanation for this discrepancy may be related to the short latitudinal distance between the study areas (less than one decimal degree), and to the lack of marked seasonality along the geographical equator, for example, in Yasuní there are no months where precipitation is <100 mm (Valencia *et al*., 2004).

Our results in the three study areas located in the southern hemisphere do not indicate a particular trend. The species activity patterns are bimodal (peaks of activity in the morning and afternoon with a decrease around midday) for the localities of Baía Das Pedras Ranch (Brazil) and Yaboti Biosphere Reserve (Argentina), but the main peak of activity occurred during different periods of the day. In Brazil, the main activity occurred in the morning, whereas in Argentina the main activity of the species was in the afternoon.

The activity patterns of tayra in Iguaçu National Park (Brazil), were unimodal and very similar to the results from localities near the geographical equator. This situation is particular because Iguaçu National Park and Yaboti Biosphere Reserve are less than 160 km away and share similar climate and terrestrial ecoregions, but the species activity patterns are completely different.

The activity patterns of tayra reported in the literature to date shows that the species has diurnal habits in different locations of central and south America. Through the analysis of 77 records of tayra obtained from a forest patch from Costa Rica and 17 records from a fragmented area (disturbed area of a matrix of pastures, crops and forest remnants) from Colombia, González-Maya *et al*. (2015) identified that tayras have a predominant diurnal activity rather than nocturnal and crepuscular activities in both study areas.

In Costa Rica the main activity of the species occurred during three periods of the day: in the morning (08:00 to 09:00 hrs), slightly after midday (12:00 to 13:00 hrs) and the afternoon (17:00 hrs). Compared with our results from Costa Rica the activity pattern of the species is almost the same even though González-Maya *et al*. (2015) analyzed the double of records of the species. In both cases the peaks of activity occurred in the early morning and late afternoon, with a slight increase around midday, this could indicate an overall consistent pattern in the activity of the species in Central America.

In Colombia the results of González-Maya *et al*. (2015) indicates that the main activity of the species occurred in different periods of the day: in the morning (08:00 to 09:00 hrs), and around noon (11:00 to 12:00 hrs). This pattern is different from that reported by Delgado *et al*. (2011) in Colombia who demonstrated that the more pronounced activity peaks occurred at noon (13:00 to 15:00 hrs, 54.5% of the records) and during the sunset (17:00 to 18:00 hrs, 36.3% of the records), and less frequently occurred between the 7:00 and 9:00 hrs (9.2% of the records). The differences of activity patterns in these locations may be due the different amount of records used in the analysis (González-Maya *et al*., 2015, n = 77; Delgado *et al*., 2011, n = 11).

In Brazilian Atlantic Forests the activity of tayra has been described as mainly diurnal (Massara *et al*., 2016, n = 76), with different peaks of activity during the first hours of the morning, the midday, and late afternoon (at this moment the activity starts to decrease), but the species remain active until midnight. These results are completely different to ours obtained in Brazil, in Baía das Pedras Ranch (n = 337) where the main activity occurred in the first hours of the morning and late afternoon, while the only peak activity of tayra in the Iguaçu National Park (n =76) occurred during midday. It is possible that activity patterns of tayra in the Atlantic Forest are influenced by the large elevation range (150 to 2,075 m asl) and the presence of potential predators including ocelots, pumas, and jaguars (Massara *et al*., 2015).

The activity of the species has been reported for three different areas in the Yungas of Argentina. The study areas (comprised of mountain jungle, and plantations with riparian forest corridors) were degraded and transformed due to the proximity to population centers and communication routes. In the analysis of 460 records of tayra obtained in the dry and rainy season, Albanesi *et al*. (2016) identified that the species is diurnal during the dry season (74% of records), with appreciable crepuscular activity (18.3% of records) and slightly inactive during midday. However, during the rainy season the tayra diurnal activity was higher (82.2%), and with less crepuscular activity. These results are similar to ours obtained in Argentina where in both cases the activity of the species was high in the morning, with a slight decrease around noon, and the biggest peak of activity in the afternoon. This could indicate a consistent pattern in the activity of the species at the southern limits of their range.

The highest percentages of diurnal activity of tayra was documented from localities near the geographical equator, in comparison with study areas located at higher latitudes. Due the species is diurnal the length of the daylight phase influences the amount of time that the species is active. It is well known that the amplitude of the annual photoperiodic cycle declines as latitude decreases, to become less than a few minutes at the equator (Gwinner & Scheuerlein, 1999), this explains the variations in the percentage of the species diurnal activity in localities far from the geographical equator, tayras remain active mainly during daylight hours. The absence of significant seasonal fluctuations in day lengths at or near the equator (Goss, 1963; 1969) implies that the species have permanently the same amount of daylight hours to remain active, which is reflected in the high percentage of diurnal activity of tayra at and near the geographical equator (Yasuni Biosphere Reserve, Ecuador Highlands, and Peruvian Amazon).

In the localities with dry season and rainy season our results indicate that the activity of tayra is essentially the same between seasons, with overlap coefficient values ranging from $\Delta_1 = 0.77$ to $\Delta_4 = 0.90$. The main resemblance is that in the four study areas the activity of the species decreased around noon during the dry season, probably due the high temperatures. However, we observed slightly differences in the study areas: 1) In Playa del Carmen and Cockscomb the activity of the species was higher in the midday during the rainy season. 2) In the UEM Nicte-Há the activity of tayra in the morning were higher in the dry season, and the activity of the species were higher during the afternoon in the rainy season. 3) In Cockscomb Basin Wildlife Sanctuary and Baía das Pedras Ranch the activity patterns of tayra between seasons was essentially the same.

Similarly, we identified that in the localities of Playa del Carmen and UEM Nicte-Há *Eira barbara* was more active in the diurnal period during the rainy season in comparison to the dry season, though this differences was not observed in the Cockscomb study area. This change may likely results from the decrease of the daytime temperatures seen during the rainy season and increased humidity, reducing risk of thermal stress during the day.

In Playa del Carmen the activity of tayra in the crepuscular period was higher during the dry season. These changes in the crepuscular activity of the species are probably because tayra must maintain more active during the crepuscular period in the dry season to compensate for the lack of activity during the day and as a strategy to be active at hours when the environmental temperature is lower. Nocturnal species may even compensate for the lost opportunity to perform an activity in darkness by increasing activity at the crepuscular period (Daly *et al.*, 1992).

In these localities, the activity of tayra during the crepuscular period was different between climatic seasons, in the UEM Nicte-Há the activity of tayra was higher in the crepuscular period during the rainy season compared with the dry season. The increase in the activity of the species in the rainy season could be influenced due to UEM Nicte-Há is located in a region subject to seasonal floods (Hidalgo-Mihart *et al*., 2017), which represents a shrinking of habitat and different availability of ecological resources.

In Cockscomb the activity of tayra in both seasons are essentially the same (the density of activity decreased around noon) with slightly differences: 1) the activity in the diurnal period was higher during the dry season and decreased during the rainy season, 2) nocturnal activity only occurred in the dry season. However, the activity during the crepuscular period had an equal percentage in both seasons.

In Baía das Pedras Ranch the activity of tayra in both seasons almost had the same distribution (the activity started to decrease right before the peak of activity ocurred) with slightly differences: 1) in the dry season the peak of activity occurred during sunrise, 2) the peak of activity in the rainy season occurred slightly later during the first hours of the morning. El Pantanal is characterized by an indistinct ever-changing boundary between water and land, seasonal fluctuations of availability of ecological resources have an impact on several aspects of the behavior and ecology of many Pantanal mammals (Alho & Silva, 2012). Although the activity patterns of tayra are almost the same between seasons, this could explained by the species plasticity and their adaptation to take advantage of food sources provided by human settlements (Hall & Dalquest, 1963).

The activity patterns of tayra in areas with climatic seasonality reported in the literature indicates that the species have different activity patterns between the dry season and the rainy season. In Colombia González-Maya *et al*. (2015) reported that the activity patterns between seasons were significantly different between seasons. The peaks of activity occurred in different periods of the day. In the dry season the main activity occurred in the first hours of the morning (08:00 to 10:00 hrs), while the in the rainy season the main activity occurred in the late afternoon.

In Argentina, Albanesi *et al.* (2016) reported that the activity of tayra at three different locations in Northwest Argentina was different between climatic seasons. Tayra were less active in the diurnal period during the dry season (74%) compared to the rainy season (82.2%), and the species was more active in the crepuscular period during the dry season (18.3%) compared to the rainy season (7.5%), the species remained slightly inactive during midday in the rainy season. The change in the activity patterns during the climatic season was not exclusive of tayra, and occurred in multiple species (*N. nasua*, *D. punctata*, *T. terrestris*, *S. brasiliensis*, *L. pardalis*, *P. tajacu* y *C. thous*) which all increased their diurnal activity during the rainy season.

Probably the most common example of the modification of the behavior of a species due to anthropogenic pressure is the change in the activity patterns. Human activity in urban areas tends to occur during daylight hours, and in response some species have changed their activity to crepuscular periods, and in some cases they have become strictly nocturnal (Ditchkoff *et al*., 2006). A large number of species of carnivore mammals have increased their nocturnal activity in the presence of anthropogenic activities, including some mustelids such as *Martes foina* (Lohrl, 1972), weasels (Curio, 1976), otters (Mason & Macdonald, 1986), and weasels and martens (Halle & Stenseth, 2000).

Tayras are habitat and diet generalists and are relatively tolerant to forest fragmentation (Canale *et al*., 2012; Massara *et al*., 2016; Mendes Pontes *et al*., 2016). Apparently, tayra are adapted to live near human settlements and take advantage of resources provided by humans in the form of gardens, orchards, sugar cane fields, and corn fields (Hall & Dalquest, 1963; Hershkovitz, 1972). Some authors have reported that when tayra live near human settlements they generally increase their crepuscular activity (Emmons & Freer, 1990, Presley, 2000).

The localities of UEM Nicte-Há, Cockscomb, Biological Corridor and Peruvian Amazon were all far from human settlements; there is no reason to think that tayra suffered anthropogenic pressure in these locations and therefore their activity patterns here likely represent what would be expected without human interference. At the Iguaçu National Park, despite its predominantly rural neighborhood, tayra were negatively affected by proximity to tourism infrastructure, based on a detailed analysis of anthropogenic effects on mammal occupancy in this locality (da Silva *et al*., 2018).

Lashley *et al*., (2018) suggest that no matter the type of camera trap records (collected in a variety of manners) the minimum number recommended to estimate activity patterns curves must be of 100 samples. Activity patterns obtained with a low sample have a lack of precision (due the diminishing accuracy of precision of estimates), for that reason the results must be interpreted with caution and moderation. As shown by the capture rates we report here, tayra are difficult to detect and records from camera traps are unfortunately accumulated slowly. Our activity patterns are here based on a range of sample sizes between 33 and 337, with only 2 study sites providing the suggested minimum of 100 samples. While we recognize that making conclusions based on the activity patterns based on low samples sizes must be done with caution, we do feel that the consistency of patterns across the data sets, regardless of sample size, indicates that our smaller data sets are likely to have adequately described the overall patterns of activity in these regions.

CONCLUSIONS

The activity patterns of *Eira barbara* summarized here and elsewhere allow us to confirm that the species has diurnal habits throughout its distribution. In localities of the northern hemisphere, the species have bimodal activity patterns with peaks of activity in the early morning and late afternoon. In populations near the geographical equator, the activity of tayra is generally unimodal; it increases progressively during the day, reaching a peak of activity at noon and decreasing in the afternoon. In southern populations, the activity of the species does not shows any consistent pattern; the activity can be unimodal (peak of activity around midday), or bimodal (with peaks or activity in the early morning and late afternoon). Our results demonstrate that the peaks of activity of the species occurs in different periods of the day across a latitudinal gradient.

This research contributes with important information about the activity patterns of tayra across their range, which represents a progress to the undestanding of the species. We are aware that the abiotic and biotic factors to which the tayra populations were different among the 10 study areas, it is necessary to integrating a full description of the characteristics of every study area to identify the effect of these variables in the activity patterns of tayra. We recommend to design the survey method specifically for tayra in order to obtain more records of the species due to their low density. These modifications will provide necessary information that will allow the analysis of the environmental variables that influence the activity patterns of tayra.

CONCLUSIÓN GENERAL

Los resultados de esta investigación demuestran que la forma (información geométrica que resulta de retirar los efectos de posición, escala y rotación de un objeto, Kendall, 1977) y tamaño del parche en la garganta es una carácter distintivo en cada ejemplar de *Eira barbara*. Esta característica sirve como un punto de referencia individual que permite identificar y diferenciar ejemplares de *Eira barbara* que posean una mancha gular.

El criterio de identificación propuesto es aplicable en toda el área de distribución de *Eira barbara* y para todas las variaciones fenotípicas descritas en la literatura, el cual puede ser utilizado en poblaciones de vida libre mediante monitoreos con cámaras trampa para generar diversas estimaciones poblacionales para la especie.

La identificación de individuos a partir de las características de la mancha gular es más sencilla en el fenotipo correspondiente a *E.b. poliocephala,* esto se debe a que la mancha gular se extiende por hombros y/o espalda. Es más sencillo identificar semejanzas o diferencias en registros laterales del animal.

Existen organismos que no tienen una mancha gular, se trata de una pequeña parte de la población, puede tratarse de una mutación en la coloración del pelaje, se recomienda hacer análisis genéticos para identificar el motivo de la ausencia de este carácter.

Se desconoce la función de la mancha gular en *Eira barbara*, es incierto si el carácter cumple alguna función de comunicación intra o interespecifica, o si solo se trata de un carácter común heredado del ancestro común de los mustélidos.

El criterio de identificación propuesto puede ser utilizado para analizar registros fotográficos de organismos de vida libre, identificar ejemplares a nivel individual y realizar descripciones poblacionales.

El criterio de identificación propuesto establece un precedente para la especie, se demostró que el criterio de identificación puede ser utilizado para identificar organismos de vida libre como en los casos de otras especies de mustélidos: *Gulo gulo* (Magoun *et al.* 2008), *Martes americana* (Sirén *et al.* 2016) y *Taxidea taxus* (Harrison, 2016).

Debido a que existen vacíos de información referente a la variación fenotípica de *Eira barbara* a través de su área de distribución, se recomienda hacer una revisión en las colecciones mastozoológicas del continente americano para generar descripciones detalladas de los diferentes fenotipos existentes y mapas de la distribución de cada uno.

Se verificó que *Eira barbara* es una especie diurna a lo largo de su distribución geográfica, se detectaron variaciones latitudinales en sus patrones de actividad. En poblaciones del hemisferio norte la actividad de la especie tiene un patrón bimodal, el principal pico de actividad ocurre en las primeras horas de la mañana, y en menor proporción durante la tarde.

En poblaciones cercanas al Ecuador geográfico la actividad de la especie es unimodal, el mayor pico de actividad ocurre al mediodía. Las poblaciones del hemisferio sur no indican una tendencia específica, la actividad fue unimodal (mayor densidad de actividad ocurrió a mediodía) o bimodal (la mayor densidad de actividad ocurrió en la mañana o en la tarde, en ambos casos la actividad disminuyó alrededor de mediodía).

Los resultados de las poblaciones cercanas al Ecuador geográfico son diferentes a los reportados en la literatura, los cuales mencionan que los picos de actividad de la especie solo ocurren en las primeras horas de la mañana y en la tarde (Kaufmann & Kaufmann, 1965; Defler, 1980; Konecny, 1989; Sunquist *et al*. 1989). Estos nuevos resultados representan un aporte al conocimiento de la especie.

La temperatura ambiental puede ser el principal factor que provoca las distintas variaciones en los patrones de actividad de *Eira barbara*. Las poblaciones alejadas del Ecuador geográfico presentan variaciones en la duración de la fase luminosa del día, al igual que cambios en la temperatura ambiental durante el día y a lo largo del año. Las poblaciones cercanas al Ecuador geográfico están expuestas a condiciones climatológicas y a un fotoperiodo constantes durante todo el año, esto puede provocar que la especie se mantenga activa durante todo el periodo diurno porque no existe riesgo de estrés térmico.

Se identificaron variaciones en los patrones de actividad de *Eira barbara* entre la temporada de lluvias y la temporada de estiaje. El incremento de la actividad diurna en algunos sitios durante la temporada de lluvia puede explicarse por la disminución de la temperatura ambiental, la cual puede provocar que la actividad de las especies aumente ya que el riesgo de estrés térmico disminuye, estos cambios en la actividad de mamíferos entre estaciones ya han sido reportados (Albanesi *et al*. 2016).

A pesar de que las características bióticas y abióticas de las diez áreas de estudio son diferentes entre sí, el coeficiente de sobreposición de actividad osciló entre $\Delta_4 = 0.64$ y $\Delta_1 = 0,95$, esto puede ser resultado de la plasticidad del *Eira barbara* para vivir en una amplia gama de hábitats, incluso cerca de asentamientos humanos (Presley, 2000).

Para poder identificar la influencia de los factores bióticos y abióticos en los patrones de actividad de *Eira barbara* se recomienda que en cada área de estudio se realice una descripción exhaustiva de las características del hábitat.

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